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Vol. 83, No. 4 October 1985

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Seattle, Washington

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Fishery Bulletin

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REGIONAL VARIATIONS IN THE GROWTH AND AGE COMPOSITION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

R. H. PARRISH,[1] D. L. MALLICOATE,[1] AND K. F. MAIS[2]

ABSTRACT

Data from the Sea Survey Program conducted by the California Department of Fish and Game were analyzed to describe regional variations in growth and age composition of northern anchovy, *Engraulis mordax*. Juvenile growth appeared to be greater at higher latitudes and in the offshore portion of the Southern California Bight. Adult growth was less variable; however, there were statistically significant differences between regions. In addition, the growth rate for the southern stock was markedly lower than that of the central stock. This difference in growth rates was used to characterize the area of overlap between the two stocks. Age composition varied with depth of water and geographical location within the Southern California Bight and with latitude. Young-of-the-year and yearling fish were found in larger proportions in shallow water and in the southern and inshore areas of the Southern California Bight. Age compositions of northern anchovies sampled in the California and Mexican purse seine fisheries were compared with those of the Sea Survey Program. This comparison suggests that the present California area restrictions, which exclude the fishery from the nearshore area, greatly reduces the number of young fish in the catch.

The purpose of this study is to describe regional variations in growth and age composition of the northern anchovy, *Engraulis mordax*. Data for the study were taken by the Sea Survey Program of the California Department of Fish and Game. Mais (1974) described this program and analyzed the data for the most common species taken in the survey. This report is an extension of Mais' work and focuses on geographical variations in age composition and growth rates and on depth variations in age composition.

Meristic and morphometric (McHugh 1951) and electrophoretic (Vrooman et al. 1981) studies on the stock structure of the northern anchovy suggest that there are three stocks (northern, central, and southern) and that the boundaries between the stocks occur in central California and central Baja California. There is also recent evidence (Parrish[3]) of a fourth stock which spawns in the fall in central California and in the northern and offshore areas of the Southern California Bight.

Mais (1974) showed that the southern stock of northern anchovies was smaller at age than the central stock. In addition, northern anchovies are known to be larger off central California than off southern California (Collins 1969; Mais 1974; Mallicoate and Parrish 1981), and they are larger in the offshore areas of the Southern California Bight than in the inshore areas (Mais 1974). These differences could be due to varying growth rates between regions, varying seasonality of spawning, varying age compositions, size-specific migration, or a combination of these factors.

Tagging experiments have shown that northern anchovies move from southern California to central California, from central California to southern California, and from southern California to Ensenada, Mexico; there is a northerly movement in summer and a southerly movement in winter (Haugen et al. 1969). Mais (1974) found northern anchovies to be distributed more offshore in some years and more inshore in other years, and he found them concentrated closer to shore and in the northern part of the Southern California Bight during the fall months. Mais (1974) suggested that northern anchovies begin an offshore and southeastward movement in late winter, which coincides with the onset of major spawning activity. These movements of anchovy may affect the measurement of growth rates and age compositions within the different regions.

METHODS

The data used in the study were taken from north-

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[3]Parrish, R. H. 1983 Evidence for a fall spawning anchovy stock. Paper presented at 1983 CalCOFI Conference.

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ern anchovies caught by midwater trawl. The gear and sampling procedures are described by Mais (1974). The data set covers the period 1966-1983 and consists of 101 cruises. Twenty-three cruises extended north of Point Conception, 77 cruises occurred in southern California and northern Baja California, and 8 cruises extended into southern Baja California. Several cruises extended into more than one region. There were a total of 4,166 trawl hauls, of which 3,017 contained anchovies. Standard lengths were normally taken from about 25 anchovies in each trawl haul in which they occurred; otoliths, for aging, were usually taken from a subsample of up to 10 fish. A total of 60,082 northern anchovies were measured, of which 20,772 were aged by California Department of Fish and Game personnel with methods developed by Collins and Spratt (1969).

For purposes of determining age composition and growth rates of northern anchovies, it was assumed that February was the birth month of all fish sampled. Anchovies off California and Baja California have a peak in spawning in February-March; however, some spawning does occur all year (Ahlstrom 1966). The age determinations used in this report are, of course, not accurate to the month. They are based on the number of annuli, the seasonality of annuli formation, an assumed February birth month, and the month the fish were caught. Annuli formation occurs in May in California (Collins and Spratt 1969). A 1-yr-old anchovy would therefore be an anchovy caught in February with no annuli on its otoliths. A 1½-yr-old anchovy would be a fish with one annuli which was caught in August. An anchovy born in February would be 15 mo old when its first annuli was formed. An anchovy spawned in September would be 8 mo old if it formed its first annuli in its first May and 20 mo old if it formed its first annuli in its second May.

Differences in growth between geographical regions were compared by linear regression analyses which included anchovies of 1½ yr of age and older. Evaluation of the relationship between age composition and water depth in the area of capture was made by grouping the samples into depth strata. The strata were established partially on the number of observations.

To determine growth rates, the data were processed with a computer program (Mallicoate and Parrish 1981) which calculates and plots the mean length, standard deviation of length, and length range by age and month. The program also tabulated the number of observations by age and month; these data were used for determining age composition.

Our preliminary analysis of the sea survey data showed an alongshore cline in the mean length of northern anchovies (Fig. 1). It also revealed a bias in the selection of fish to be aged. Aged fish were generally larger at all latitudes than were the unaged fish. This bias is apparently due to a consistent tendency for samplers to pick larger anchovies for the subsample which was aged. Anchovies < 100 mm SL were particularly susceptible to not being selected for aging (Table 1). On checking with the field biologists who took the data, we found a second source of bias which occurred only in trawl hauls of exclusively small fish. When trawl hauls were considered by the sampler to be "obviously" all young-of-the-year fish, there was a tendency not to take otoliths for age determination. These sampling biases affect the analyses of age composition presented in this report but do not affect the growth analyses.

TABLE 1.—Two types of length bias in sampling northern anchovies in the Sea Survey Program.

Standard length (mm)	No. fish measured	No. fish measured in hauls sampled for otoliths	No. otolith samples	[1]Bias 1	[2]Bias 2
<70	2,174	1,275	460	0.59	0.36
70-80	2,366	1,939	684	0.82	0.35
80-90	4,667	4,241	1,667	0.91	0.39
90-100	7,077	6,367	2,498	0.90	0.39
100-110	8,988	7,875	2,997	0.88	0.38
110-120	12,058	10,834	4,164	0.90	0.38
120-130	11,744	10,462	4,215	0.89	0.40
130-140	7,390	6,456	2,748	0.87	0.43
140+	3,619	3,036	1,339	0.84	0.44
Total	60,082	52,484	20,772		

[1]Bias 1 is the decision to sample for otoliths (i.e., the proportion of fish in trawl hauls which were sampled for otoliths).

[2]Bias 2 is the selection of larger fish by the sampler (i.e., the proportion of fish in trawl hauls, which were sampled for otoliths, for which otolith samples were taken).

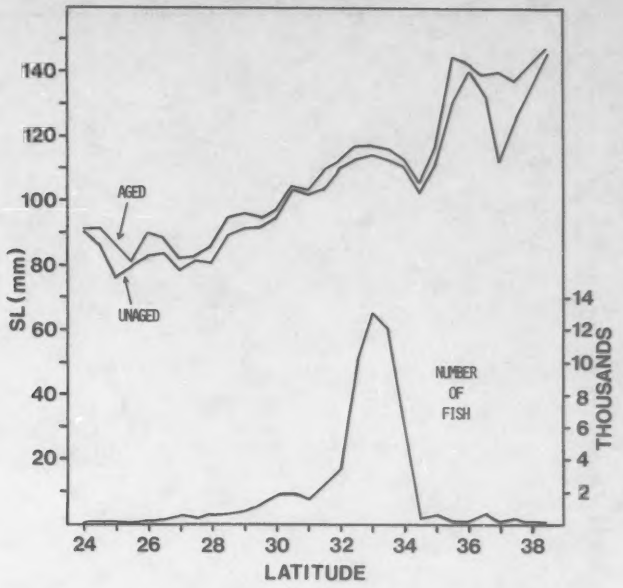

FIGURE 1.—Mean length of aged and unaged northern anchovies and the number of anchovies by half degree of latitude.

The data were inadequate to calculate growth curves or age composition on the one-half degree of latitude interval used in Figure 1; therefore, geographical regions were selected based partially on the number of observations. For example, the southern and central Baja California and central California areas, which had fewer samples, were more widely spaced than the southern California and northern Baja California areas. Nearly all of the anchovy samples taken south of lat. 32°N or north of lat. 34°N were taken within one-half degree of the coast. The lat. 32°34°N area included a large amount of samples taken further than one-half degree from the coast. This area, the Southern California Bight, contains numerous islands and basins; we, therefore, divided it into regions which approximate the natural basins described in Emery (1954) (Fig. 2).

RESULTS

Growth

Earlier studies on northern anchovies from British Columbia (Pike 1951), northern California (Waldvogel 1977), central California (Clark and Phillips 1952), and southern California (Spratt 1975) showed considerable variation in their growth (Fig. 3A). Anchovies in British Columbia, lat. 49°N, and northern California, lat. 41°N, are of the northern stock (Vrooman et al. 1981) and have a summer spawning season. Anchovies in southern California, lat. 33°N, are of the central stock, whereas those in central California, lat. 36°N, are considered to be a mixture of northern and central stocks (Vrooman et al. 1981); anchovies in both southern and central California have a late winter (February-April) spawning season (Parrish footnote 3). Anchovies in British Columbia were the fastest growing of all the four areas in their first year of life, whereas anchovies in northern California were the slowest. Anchovies in central and southern California showed similar growth rates after their first year of life; however, the growth rate of anchovies in central California was greater than the growth rate of those in southern California in their first year.

Our study shows that the growth of anchovies has a distinct geographical pattern. Anchovies sampled in the Central California region (CC) and the offshore area of the Southern California Bight [i.e., San Nicolas (SN) and Tanner and Cortez Banks (TCB) regions] have the fastest juvenile growth (Fig. 3). Anchovies in these areas attain an average length of 120 mm before they are 1½ yr old. In the inshore areas of the Southern California Bight and in Baja California there is a continuous decline in the growth rate associated with decreasing latitude (Figs. 3, 4). Anchovies reach a mean length of 120 mm at about age 2 in the Santa Barbara Channel region (SBC)

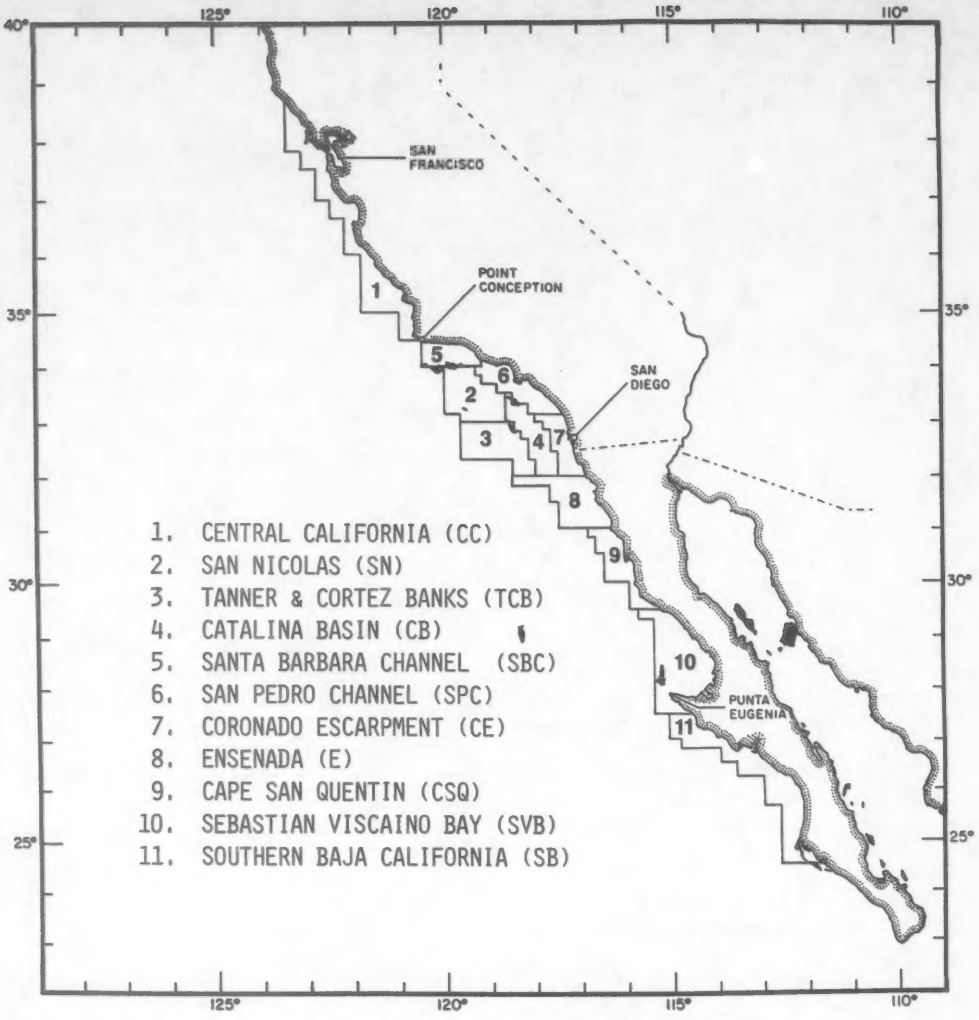

FIGURE 2.—Geographical regions for which the growth and age composition of northern anchovies were determined.

and in the remaining offshore region, Catalina Basin (CB). In the San Pedro Channel (SPC), Coronado Escarpment (CE), and Ensenada (E) regions anchovies reach 120 mm at about age 3. In the Cape San Quentin (CSQ) and Sebastian Viscaino Bay (SVB) regions anchovies reach 120 mm at about age 4 or later.

The Cape San Quentin (CSQ), Sebastian Viscaino Bay (SVB), and Southern Baja California (SB) regions include anchovies from both the central and southern stocks, and there are marked differences in their growth (Fig. 4). Anchovies from the southern stock appear to reach an asymptotic mean size of about 92 mm, whereas those from the central stock continue to grow throughout their lives. Note the occurrences of 2- to 4-yr-old fish with monthly mean lengths of about 92 mm (Fig. 4 CSQ, SVB, SB). Assuming that stocks can be identified by size at age, the Cape San Quentin region appears to be dominated by the central stock; however, the

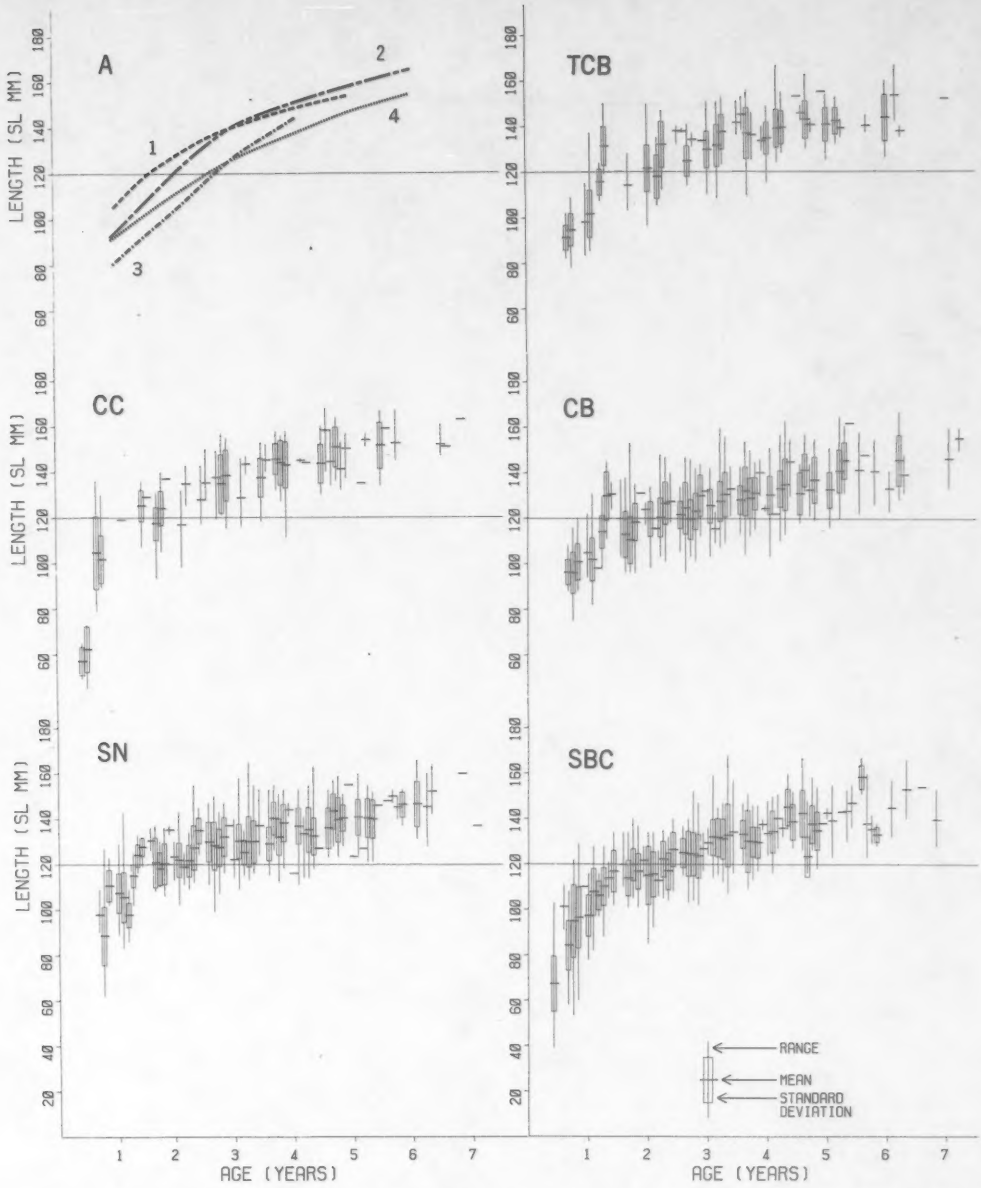

FIGURE 3.—Age-length relationships of northern anchovies taken in A. Earlier studies 1) British Columbia (Pike 1951), 2) Central California (Clark and Phillips 1952), 3) Northern California (Waldvogel 1977), and 4) Southern California (Spratt 1975), CC, Central California; SN, San Nicolas; TCB, Tanner and Cortez Banks; CB, Catalina Basin; SBC, Santa Barbara Channel.

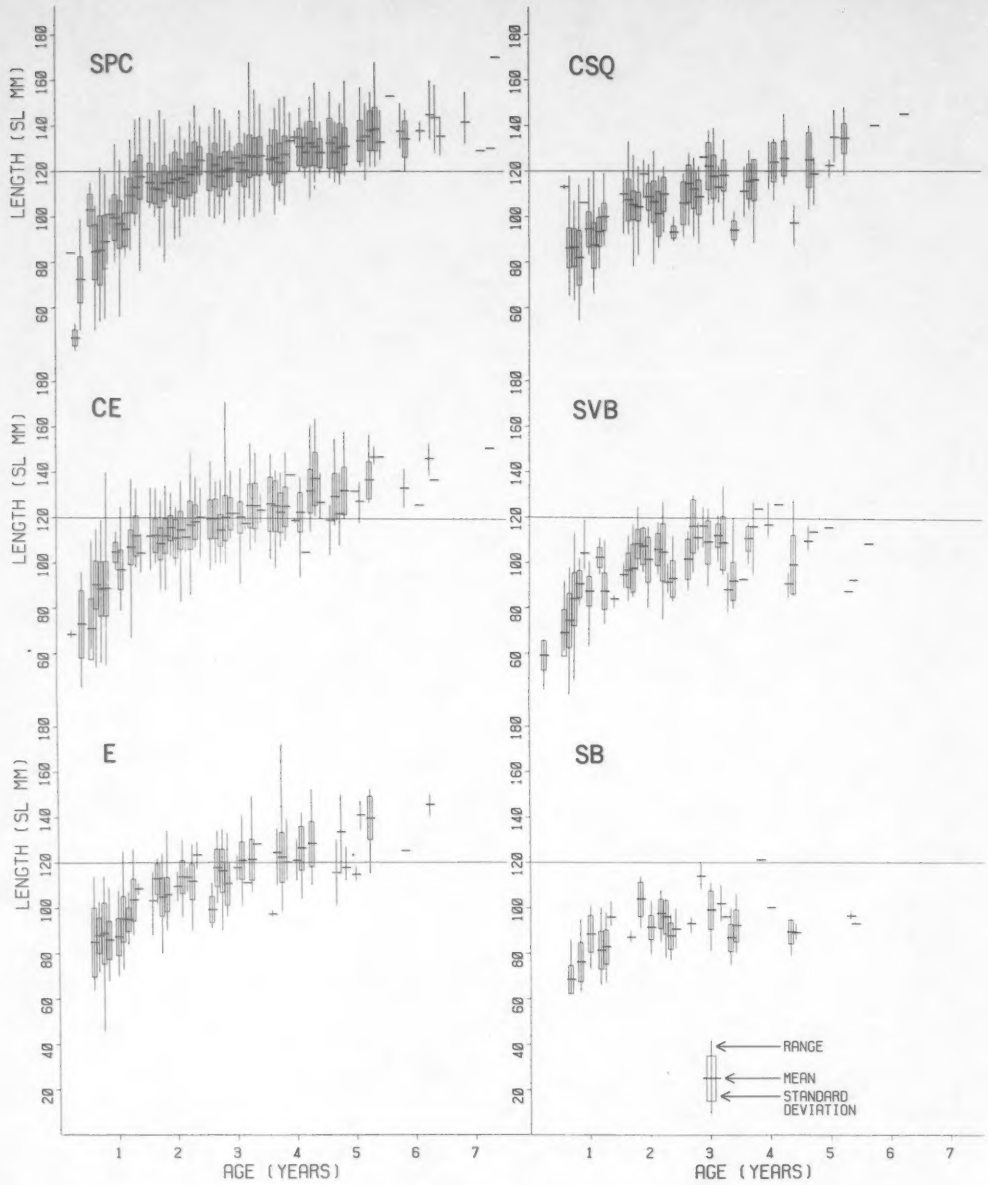

FIGURE 4.—Age-length relationships of northern anchovies taken in SPC, San Pedro Channel; CE, Coronado Escarpment; E, Ensenada; CSQ, Cape San Quentin; SVB, Sebastian Viscaino Bay; and SB, Southern Baja California.

southern stock does extend into this region. The most northerly trawl sample which could be identified, by size at age, as southern stock was a June 1971 sample taken at lat. 30.3°N. Southern and central stock anchovies broadly overlap in the Sebastian Viscaino Bay region; however, the region is occupied principally by the southern stock in the summer and by the central stock in the fall and winter. The Southern Baja California region is dominated by the southern stock; however, central stock anchovies, as identified by size at age, were taken as far south as lat. 26.5°N in November 1967. The fact that the central stock is the farthest south in winter and the southern stock the farthest north in summer suggests that the separation of the stocks is aided by different environmental preferences, possibly temperature.

The Central California region is an area of overlap between the northern and central anchovy stocks. In addition, as previously mentioned (Parrish footnote 3), a fall spawning stock may occur in central California and the offshore areas of the Southern California Bight. Vrooman et al. (1981) did not have any samples south of Monterey in central California or from the offshore and northern areas of the Southern California Bight. Samples from these areas may consist of a mixture of different stocks with different spawning seasons. Our assumption of a February birth month in these areas must therefore be evaluated.

Regression Analysis

Growth in length of anchovies in the size range sampled by the Sea Survey Program (i.e., 40-180 mm SL) can be divided into two phases. The early, juvenile phase extends until the fish are about 1 yr old. Methot (1981) found that in the Southern California Bight juvenile growth averages about 9 mm/mo, and it is at a maximum when the fish are between 40 and 50 mm SL. The second, adult phase extends from a little over 1 yr old until death. Growth during this phase is more than an order of magnitude less than the early phase (i.e., 0.48-0.69 mm/mo). Examination of the age-length relationships (Figs. 3, 4) in the central stock shows that growth in the adult phase is essentially linear. Therefore, we used linear regressions to compare growth of anchovies from different regions. These analyses included only fish of 1½ yr of age and older. This model has several advantages for comparing the growth during the two phases described above. By limiting the model to the linear segment of the age-length relationships, the slopes of the regressions can be used to compare the regional variations in growth rate during the adult phase. Another advantage is that the expected length at 1½ yr of age can be used to compare regional variation in growth during the juvenile phase.

Juvenile Growth

In the area occupied by the central stock, growth during the juvenile phase shows considerable variation among regions. There were significant differences in growth to age 1½. Fastest growth occurred in the north, and the slowest was in the south (Table 2, Fig. 5). Mean standard length at 1½ yr of age was 123.6 mm in the Central California region, 113.4 mm in the San Pedro Channel region, and 103.6 mm in the Cape San Quentin region. The three southernmost Baja California regions contain mixtures of the central and southern stocks; therefore, data from these regions were divided into central and southern stock sets, based on length and month, for the analyses. In contrast to those of the central stock, anchovies of the southern stock attain only 91.8 mm by age 1½. Within the Southern California Bight there is also an inshore-offshore gradient, with faster juvenile growth in the offshore regions and slower growth in the inshore regions (i.e., lengths at age 1½ in the Coronado Escarpment, Catalina Basin, and Tanner and Cortez Banks regions were 110.5, 116.4, and 119.2 mm respectively).

An analysis of covariance showed that the differences in size at age 1½ are not significantly different ($\alpha = 0.01$) in two pairs of regions. The San Nicolas region (120.4 mm at age 1½) and the Tanner and Cortez Banks region (119.2 mm) are the first pair, and the Catalina Basin region (116.4 mm) and the Santa Barbara Channel region (116.2 mm) are the second pair. In all other pairs of regions, size at age 1½ is significantly different at the $\alpha = 0.0001$ level.

Adult Growth

The regressions demonstrate that growth during the adult phase is relatively constant between the different regions occupied by the central stock, with slopes varying from a low of about 6 mm/yr to a high of about 8 mm/yr (Table 2). In contrast, anchovies of the southern stock have essentially no adult growth after age 1½ (i.e., slope = 0.07 mm/yr).

Although the differences in adult growth between regions is not large, there are statistically significant differences (Table 3). The San Nicolas region and the Tanner and Cortez Banks region have adult growth

TABLE 2.—Regression parameters and statistics for the relationship between age and length of northern anchovies older than 1½ yr: Central California (CC), San Nicolas (SN), Tanner-Cortez Banks (TCB), San Nicolas combined with Tanner-Cortez Banks (SN+TCB), Catalina Basin (CB), Santa Barbara Channel (SBC), Catalina Basin combined with Santa Barbara Channel (CB+SBC), San Pedro Channel (SPC), Coronado Escarpment (CE), Ensenada (E), Cape San Quentin (CSQ), Sebastian Viscaino Bay and Southern Baja California, central stock only (SVB+SB), and Southern Baja California, southern stock only (S).

Area	Mean age (Yr)	Mean length (SL mm)	Length at age 1½ (SL mm)	Adult growth (mm/yr)	*r*	SD of length at age 1½	SD of adult growth	*N*
				Central Stock				
CC	3.4	138.4	123.6	7.75	0.702	1.563	0.431	335
SN	3.3	131.1	120.4	5.97	0.613	0.713	0.205	1,410
TCB	3.2	130.8	119.2	6.69	0.623	0.975	0.286	860
SN+TCB	3.3	131.0	120.0	6.23	0.616	0.577	0.167	2,270
CB	3.1	126.7	116.4	6.29	0.582	0.633	0.192	2,092
SBC	2.9	125.6	116.2	6.83	0.636	0.689	0.224	1,374
CB+SBC	3.0	126.3	116.4	6.50	0.606	0.465	0.145	3,466
SPC	2.8	121.3	113.4	6.07	0.575	0.435	0.146	3,497
CE	2.7	118.7	110.5	6.89	0.569	0.666	0.235	1,798
E	2.8	116.5	106.2	8.08	0.636	0.944	0.321	934
CSQ	2.5	111.1	103.6	7.54	0.649	0.776	0.291	923
SVB+SB	2.4	106.4	101.1	5.76	0.443	1.571	0.618	358
				Southern Stock				
S[1]	2.9	91.9	91.8	0.07	0.009	1.274	0.421	335

[1]Combined from three areas: CSQ, SVB, and SB.

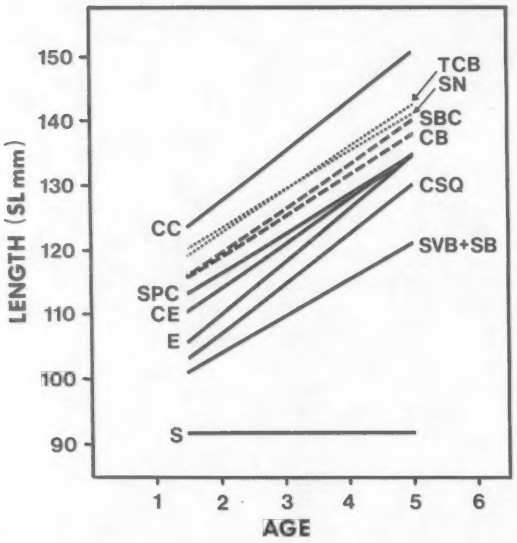

FIGURE 5.—Linear regressions showing the expected length at age (Table 1) of northern anchovies taken in CC, Central California; SN, San Nicolas; TCB, Tanner and Cortez Banks; CB, Catalina Basin; SBC, Santa Barbara Channel; SPC, San Pedro Channel; CE, Coronado Escarpment; E, Ensenada; CSQ, Cape San Quentin; SVB+SB, Sebastian Viscaino Bay and Southern Baja California, central stock only; and S, Southern Baja California, southern stock only.

patterns which are not statistically different (α = 0.01), and since the two regions are adjacent we have considered them together. Also there is no significant difference (α = 0.01) in adult growth in the Catalina Basin and the Santa Barbara Channel regions, but since these regions are geographically separated we have retained them as separate regions. The relatively large standard deviations of the regression slopes (Table 2) for fish from the Central California and the Sebastian Viscaino Bay and the Southern Baja California regions may indicate that these regions are the most likely to have mixtures of more than one stock.

There was no significant difference (α = 0.01) between growth of adults in the best growth regions (Ensenada, Cape San Quentin, and Central California). The difference between the Coronado Escarpment and the Santa Barbara Channel regions is not significant at the α = 0.1 level nor are the differences between the Catalina Basin, combined San Nicolas-Tanner and Cortez Banks, San Pedro Channel, and combined Sebastian Viscaino Bay and Southern Baja California regions.

Tanner and Cortez Banks, and Catalina Basin) differ from the other regions in that they are dominated by fish 3 yr and older (Fig. 6A, Table 4). Central California and Tanner and Cortez Banks also have substantial percentages of young-of-the-year fish, whereas the other two regions do not.

Anchovies in the three inshore regions of the Southern California Bight (Santa Barbara Channel, San Pedro Channel, and the Coronado Escarpment) have very similar age compositions (Fig. 6B, Table 4). One- and two-yr-old fish are the most numerous in these three regions. Young-of-the-year and 3 yr-olds are slightly less abundant than 1- and 2-yr-olds, and there are fewer older fish in the samples.

Baja California is characterized by a dominance of young fish (Fig. 6C, Table 4). The age compositions in the Ensenada, Cape San Quentin, and Sebastian Viscaino Bay regions are very similar; young-of-the-year and 1-yr-old fish are the most abundant, and there is rapid decrease in the abundance of fish with increasing age. Anchovies in southern Baja California are principally from the southern stock. The age composition in this region shows a preponderance of 1-yr-olds, and like the other Baja California regions there are few fish of age 4 or older.

TABLE 3.—Significance levels for differences in growth of adult northern anchovies from different geographical regions: Ensenada (E), Central California (CC), Cape San Quentin (CSQ), Coronado Escarpment (CE), Santa Barbara Channel (SBC), Tanner and Cortez Banks (TCB), Catalina Basin (CB), San Nicolas combined with Tanner and Cortez Banks (SN+TCB), San Pedro Channel (SPC), San Nicolas (SN), Sebastian Viscaino Bay and Southern Baja California, central stock only (SVB+SB), and Southern Baja California, southern stock only (S). Geographic areas are arranged in order from largest to smallest slopes.

Area	E	CC	CSQ	CE	SBC	TCB	CB	SN+TCB	SPC	SN	SVB+SB	S
E	—											
CC	0.5573	—										
CSQ	0.2217	0.6517	—									
CE	0.0019	0.0514	0.0754	—								
SBC	0.0015	0.0477	0.0629	0.9422	—							
TCB	0.0013	0.0331	0.0384	0.6516	0.6951	—						
CB	0.0000	0.0000	0.0000	0.0605	0.0628	0.2400	—					
SN+TCB	0.0000	0.0003	0.0002	0.0283	0.0280	0.0000	0.8141	—				
SPC	0.0000	0.0000	0.0000	0.0015	0.0033	0.0465	0.3560	0.4659	—			
SN	0.0000	0.0000	0.0000	0.0042	0.0042	0.0367	0.2547	0.3234	0.6902	—		
SBV+SB	0.0000	0.0085	0.0051	0.0826	0.0952	0.1616	0.3943	0.4372	0.6048	0.7379	—	
S	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	—

Age Composition by Area

Geographical variation in age composition is one factor which could influence the observed variation in mean size of anchovies in the various regions; therefore, age composition was calculated for each of the regions used earlier (Fig. 2). Few anchovies < 60 mm SL occur in the data, and it appears that young-of-the-year fish are apparently not susceptible to capture by the midwater trawl gear used in the sea survey until they are about 6 mo old.

Central California and the three offshore regions within the Southern California Bight (San Nicolas,

Age Composition by Depth Strata

Anchovies primarily live within the upper mixed layer; they occur in the surface layer over the continental shelf and over deepwater regions. Mais (1974) showed that the average size of anchovies sampled in offshore areas was greater than that of anchovies sampled near the coast. The percentage of trawl hauls containing anchovies was quite constant in areas with different water depths, varying

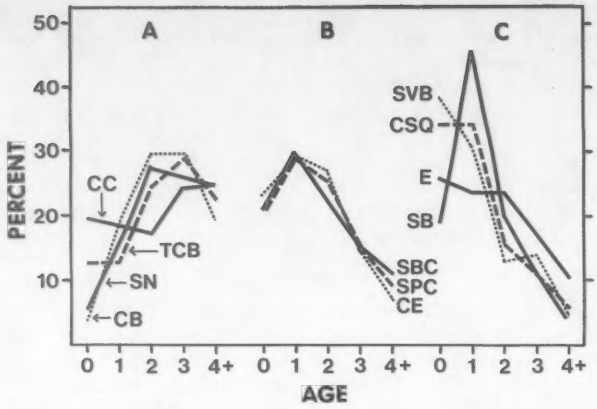

FIGURE 6.—Age composition of northern anchovies taken in the following geographical regions: A. Central California and offshore areas of the Southern California Bight; Central California (CC), San Nicolas (SN), Tanner and Cortez Banks (TCB), and Catalina Basin (CB); B. Inshore areas of the Southern California Bight; Santa Barbara Channel (SBC), San Pedro Channel (SPC), and Coronado Escarpment (CE); C. Baja California; Ensenada (E), Cape San Quentin (CSQ), Sebastian Viscaino Bay (SVB), and Southern Baja California (SB).

TABLE 4.—Percentage age composition of northern anchovies by geographical region: Central California (CC), San Nicolas (SN), Tanner-Cortez Banks (TCB), Catalina Basin (CB), Santa Barbara Channel (SBC), San Pedro Channel (SPC), Coronado Escarpment (CE), Ensenada (E), Cape San Quentin (CSQ) Sebastian Viscaino Bay (SVB), Southern Baja California (SB).

	Age							No.
Area	0	I	II	III	IV	V	VI+	fish
CC	19.3	17.2	14.7	23.9	17.7	5.7	1.6	436
SN	5.6	15.5	27.7	26.0	15.9	7.4	2.0	1,721
TCB	12.6	12.6	24.3	28.3	13.6	6.5	2.1	1,136
CB	3.7	18.7	29.2	29.2	12.8	5.2	1.1	2,538
SBC	21.8	29.6	22.2	15.2	8.2	2.4	0.6	1,989
SPC	21.6	28.6	25.4	15.6	6.3	1.9	0.5	5,439
CE	23.5	28.1	26.9	14.6	5.4	1.3	0.2	2,965
E	25.8	23.6	23.4	17.1	7.6	2.3	0.2	1,464
CSQ	33.8	33.7	15.5	11.2	4.4	1.2	0.1	1,779
SVB	38.1	30.8	12.8	13.5	4.5	0.3	—	896
SB	18.8	45.7	19.6	11.5	3.7	0.7	—	409

between 64 and 77% (Table 5). This is probably influenced by the fact that trawling (in the upper 30 m) was carried out normally in areas where fish schools had already been detected by depth recorder or sonar.

In southern California (lat. 32°34°N) young-of-the-year anchovies comprise more than one-half of the anchovies sampled in the 5-25 fathom-depth stratum (Table 6A). One- and two-yr-olds comprise more than one-half of the anchovies in the 26-50, 51-150, 151-300, and 301-500 fathom strata. The most abundant age group in the 26-50 stratum is age 1; there are essentially equal numbers of age 1 and age 2 anchovies in the 51-150 and 151-300 strata; 2-yr-olds are the most abundant age group in the 301-500 stratum; and 3-yr-olds are the most abundant age group in the 701+ stratum. Age groups 3-6+ each show an increasing percentage with increasing depth. Collectively they comprise about 11% of the 5-25 stratum, 31% of the 51-150 stratum, and 51% of the 701+ stratum. The same general pattern occurs in northern Baja California (lat. 29.5°32°N); however, the percentage of young fish declines more

TABLE 5.—Percentage of midwater trawl hauls taking northern anchovies by depth strata. Trawl hauls were normally within 30 meters of the surface.

Depth (fm)	Total sets	% sets with anchovies
5-25	704	75
26-50	828	69
51-150	554	69
151-300	546	76
301-500	752	77
501-700	437	73
701+	345	64
Total	4,166	72

TABLE 6.—Age composition (%) of northern anchovies taken in shallow and deep-water areas (depth in fathoms).

A

		Lat. 32°-34°N						
Age	Depth:	5-25	26-50	51-150	151-300	301-500	501-700	701+
0		56.5	26.3	16.9	7.8	5.5	3.0	6.5
I		20.6	29.5	26.5	27.4	25.8	17.9	15.5
II		12.5	24.1	26.0	27.9	30.6	32.0	26.8
III		7.0	12.3	20.1	22.8	22.7	28.2	27.1
IV		2.5	5.8	6.8	9.1	10.5	13.3	15.3
V		0.8	1.5	3.2	3.6	3.8	4.9	7.2
VI+		0.2	0.5	0.6	1.4	1.1	0.6	1.7
n		1,579	1,492	1,102	2,199	3,704	2,091	1,086

B

		Lat. 29.5°-32°N			
Age	Depth:	5-25	26-50	51-150	151+
0		56.1	36.8	21.0	8.9
I		23.1	40.4	28.5	28.8
II		12.3	10.8	24.2	26.9
III		6.2	7.8	14.2	23.3
IV		1.9	3.6	9.4	8.7
V		0.3	0.6	2.5	3.0
VI+		—	—	0.2	0.3
n		935	619	480	1,189

C Aug.-Dec.

		Lat. 29.5°-32°N				Lat. 32°-34°N			
Age	Depth:	5-25	26-50	51-150	151+	5-25	26-50	51-150	151-300
0		62.8	52.6	38.7	24.9	66.2	37.8	26.4	16.0
I		18.2	32.3	29.2	43.0	15.6	29.0	24.7	21.0
II		11.7	10.6	19.9	24.4	12.1	22.5	25.8	32.4
III		5.7	4.0	8.2	6.4	5.0	8.6	16.1	21.2
IV		1.6	0.5	4.1	1.2	0.9	2.0	5.1	8.3
V		—	—	0.7	—	0.2	0.1	1.8	0.9
VI+		—	—	—	—	—	—	—	0.2
n		806	378	267	405	1,286	1,013	546	990

slowly with increasing depth there than in southern California (Table 6B). In both southern California and northern Baja California, there is a direct relationship between average age and depth of water in which fish were caught. In the period August-December when smaller (< 60 mm) anchovies can be caught by midwater trawls, there is a greater dominance of young-of-the-year fish in the shallower water (Table 6C). In the northern Baja California area, 63% of the 5-25 stratum and 53% of the 25-50 stratum were young-of-the-year fish. In southern California the corresponding percentages were 66 and 38.

Sea Survey - Fishery Comparisons

The purse seine fleets which harvest anchovies operate primarily out of San Pedro, California, and Ensenada, Mexico. The age composition of anchovies in the San Pedro fishery (Mallicoate and Parrish 1981) contains a smaller proportion of age 0 and age 1 fish than does the sea survey data for the San Pedro Channel region. We only had 2 years of age composition data for the Ensenada fishery available to us (Sunada and Silva 1980), but this limited information shows the same dominance of younger anchovies as in the sea survey data for this region. The San Pedro fishery had several regulations which reduced the numbers of young fish in the catch. These included a 5-in minimum size limit and a series of area closures which prevent the fleet from fishing in nearshore areas. The Ensenada fishery did not have regulations which influenced the age composition of the catch.

To evaluate the effects of the area closures and size limit on the San Pedro fishery, we broke the sea survey data into depth classifications, < 50 fathoms and > 50 fathoms. The > 50 fathom classification was intended to approximate the area of the fishery (i.e., the coastal strip is excluded). In this area the

age composition of anchovies taken by the Sea Survey Program is very close to that taken by the fishery; conversely, the age composition of the fishery is unlike that taken in areas < 50 fathoms (Fig. 7). The California fishery no longer has a 5-in size limit; however, the closure of the nearshore area appears to be the dominant factor in reducing the catch of young anchovies.

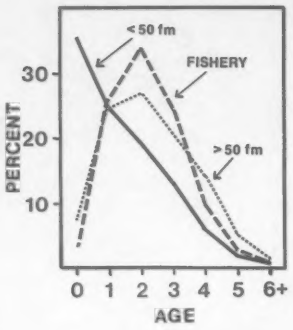

FIGURE 7.—Comparison of the age composition of northern anchovies taken in the San Pedro purse seine fishery with those taken in areas with <50 fathoms and >50 fathoms of water in the midwater trawl Sea Survey Program.

DISCUSSION

Our data show that the growth rate and the age composition of northern anchovies vary geographically. The greatest differences in growth appear to occur during the juvenile stage; growth in adults shows much less regional variation. Juvenile growth is greatest in central California and in the offshore areas of the Southern California Bight. In the inshore regions there is a trend toward reduced juvenile growth from central California to southern Baja California. Average size at age 1½ falls from 123.6 mm to 91.8 mm over this area. Growth in adult anchovies appears to be the greatest in northern California, and it is also relatively high in British Columbia (Pike 1951), central California, and northern Baja California. Adult growth appears to be relatively low in the Southern California Bight; this, however, may be an artifact as this area probably includes resident fish plus slower growing fish which have moved into this region from the south. Age composition showed a large variation among regions, and the pattern of this variation appears to be closely related to the gyral circulation within the Southern California Bight. There is also a strong relationship in age composition to the depth of water at trawl sites. Adult anchovies dominated the catches in the offshore, deepwater regions of the Southern California Bight and in central California. Age also had a strong latitudinal gradient with adult fish dominating in the north and young-of-the-year and yearling fish dominating in the shallow water areas off central and northern Baja California. Adult anchovies appear to be concentrated in areas of the Bight where prevailing currents will result in southerly and inshore larval transport (Parrish et al. 1981). At recruitment, anchovies appear to be heavily concentrated in shallow water, and young fish appear to be concentrated in the nearshore area where they will tend to be advected northward by the southern California gyre.

As will be discussed later, the interpretation of the regional differences in juvenile growth is dependent upon the stock structure in the various regions. Earlier studies (McHugh 1951; Vrooman et al. 1981) showed that the boundary between the southern and central stocks was in the northern Sebastian Viscaino Bay area. This is supported by the present study, and, as previously mentioned, the boundary is further north in the summer and fall and further south in winter and spring. We feel that there is ample evidence that the southern stock had the smallest juvenile growth rate and that growth during the adult phase is minor. Vrooman et al. (1981) suggested that the boundary between the northern and central stocks occurs in the central California area; both northern and central stocks occurred in samples taken at San Francisco (lat. 37°50′N) and Monterey (lat. 36°50′N). Their data might be interpreted to suggest that a fourth stock occurred in the San Francisco and Monterey samples, and in addition it has been suggested (Parrish footnote 3) that this fourth stock spawns during the fall in central California and the offshore areas of the Southern California Bight. Unfortunately the Vrooman et al. (1981) study did not have any samples from the region between Monterey (lat. 36°50′N) and Newport (lat. 33°30′N), nor were there any samples from the offshore areas of the Southern California Bight. It is therefore not presently possible to determine the amount of stock mixture over much of the accepted range of the central stock.

Variation in juvenile growth of northern anchovies in the different regions may be due to genetic factors, differences in the seasonality of spawning, or environmental factors. The northern stock has a relatively short spawning season with a strong peak in July (Richardson 1980). The central stock has a

more extended spawning season with a broad peak from February to April, and there is some spawning all year in the central stock region. It is not yet known if the anchovies that spawn in central and southern California during the summer and fall are from the central stock, northern stock, or a possible fall spawning stock. If the anchovies in this region are predominatly from the central stock, the relatively high juvenile growth in central California and the offshore portion of the Bight might be due to a favorable feeding environment. Offshore portions of the Southern California Bight have been shown to have considerably more plankton and nutrients than the inshore portions (Reid et al. 1958; Owen 1980). If the anchovies in the area occupied by the central stock have a large component that are not central stock, the increased juvenile growth could be due to the genetic differences, due to environmental differences, or caused by the assumption of a February birth month. At our "assumed" age of 1½ yr, an anchovy spawned in the fall would be about 6 mo older than the "normal" central stock anchovy. If the growth that occurred during these additional 5 mo was at the normal adult rate (i.e., 0.48-0.69 mm/mo), there would be only a 2-4 mm difference in the size of the two fish. However, the difference in mean length between 1½-yr-old anchovies in the central California and Cape San Quentin regions is 20 mm. If, however, growth during the 5 mo is even one-half of the average juvenile rate (i.e., 9 mm/mo) the difference in size at "1½" yr could be achieved.

CONCLUSION

The interpretation of regional variations in the growth and age composition of northern anchovies in the area between central California and central Baja California and the implications of this study for fisheries management are dependent upon the stock structure of the anchovies in the area.

If a significant proportion of these fish are not from the central stock, this study suggests the following:

1. The observed regional variation in age composition may be the result of mixtures of stocks with different mortality rates.
2. The juvenile growth rate of anchovies in the central stock is lower than that of anchovies from the northern stock(s). The reason for this lower growth rate could be either genetic, environmental, or dependent upon the seasonality of spawning.
3. The southern California and Mexican fisheries are based on different stock mixtures, and thus the interactions between these fisheries would not be as great as they would be if both were based entirely on the same stock.

If essentially all of these anchovies are from the central stock, this study suggests the following:

1. The offshore regions of the Southern California Bight contain a disproportionate share of the adult anchovies; however, recruitment does not occur here to any significant extent.
2. Recruitment occurs largely in shallow water along the coast, and the northern Baja California region has the largest percentage share of young-of-the-year anchovies.
3. Larvae and juveniles recruited from the offshore regions of the Southern California Bight tend to move or be advected south and inshore.
4. The relatively high juvenile growth rates in central California and the offshore regions of the Southern California Bight are due to favorable environmental conditions.
5. As they grow older anchovies tend to move, or be advected, north and offshore.
6. Mixing of adults is not complete; otherwise length at age and age composition would be the same everywhere.
7. Due to the inferred tendency for recruitment to occur in the south, an extensive fishery on the central stock would reduce the proportion of older anchovies and result in fewer older anchovies in the northern and offshore areas.
8. The combination of the large Mexican fishery, which has been associated with a reduction in the proportion of older anchovies (Mais 1982), and the continued closure of the nearshore areas where younger fish are concentrated will severely impact the California fishery.

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LITERATURE CITED

AHLSTROM, E. H.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current Region off California and Baja California, 1951-64: A summary. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 534, 71 p.

CLARK, F. N., AND J. B. PHILLIPS.
1952. The northern anchovy (*Engraulis mordax*) in the California fishery. Calif. Fish Game 38:189-207.

COLLINS, R. A.
1969. Size and age composition of northern anchovies (*Engraulis mordax*) in the California anchovy reduction fishery for the 1965-66, 1966-67, and 1967-68 seasons. Calif. Dep. Fish Game Fish Bull. 147:56-74.

COLLINS, R. A., AND J. D. SPRATT.
1969. Age determination of northern anchovies, *Engraulis mordax*, from otoliths. Calif. Dep. Fish Game Fish Bull. 147:39-55.

EMERY, K. O.
1954. Source of water in basins off southern California. J. Mar. Res. 13:1-21.

HAUGEN, C. W., J. D. MESSERSMITH, AND R. H. WICKWIRE.
1969. Progress report on anchovy tagging off California and Baja California, March 1966 through May 1969. Calif. Dep. Fish Game Fish Bull. 147:75-89.

MAIS, K. F.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game Fish Bull. 162:1-79.
1981. Age-composition changes in the anchovy, *Engraulis mordax*, central population. Calif. Coop. Oceanic Fish. Invest. Rep. 22:82-87.

MALLICOATE, D. L., AND R. H. PARRISH.
1981. Seasonal growth patterns of California stocks of northern anchovy, *Engraulis mordax*, Pacific mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*. Calif. Coop. Oceanic Fish. Invest. Rep. 22:69-81.

MCHUGH, J. L.
1951. Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*). Bull. Scripps Inst. Oceanogr. 6:123-160.

METHOT, R., JR.
1981. Growth rates and age distributions of larval and juvenile northern anchovy, *Engraulis mordax*, with inferences on larval survival. Ph.D. Thesis, Univ. California, San Diego, 388 p.

OWEN, R. W.
1980. Eddies of the California Current System: physical and ecological characteristics. *In* D. M. Power (editor), The California Islands: Proceedings of a multidisciplinary symposium, p. 237-263. Santa Barbara Mus. Nat. Hist. (Calif.).

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

PIKE, G. C.
1951. Age, growth and maturity studies on the Pacific anchovy (*Engraulis mordax*) from the coast of British Columbia. M.A. Thesis, Univ. British Columbia, Vancouver, 44 p.

REID, J. L., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current System. Calif. Coop. Oceanic Fish. Invest. Rep., 1 July 1956 to 1 January 1958, p. 28-56.

RICHARDSON, S. L.
1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.

SPRATT, J. D.
1975. Growth rate of the northern anchovy, *Engraulis mordax*, in southern California waters, calculated from otoliths. Calif. Fish Game 61:116-125.

SUNADA, J. S., AND S. SILVA.
1980. The fishery for northern anchovy, *Engraulis mordax*, off California and Baja California in 1976 and 1977. Calif. Coop. Oceanic Fish. Invest. Rep. 21:132-138.

VROOMAN, A. M., P. A. PALOMA, AND J. R. ZWEIFEL.
1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. Calif. Fish Game 67:39-51.

WALDVOGEL, J. B.
1977. Age, maturity and distribution of northern anchovy *Engraulis mordax* in Humboldt Bay, California. M.S. Thesis, Humboldt State Univ., Arcata, CA, 36 p.

PARASITES OF BENTHIC AMPHIPODS: MICROSPORIDANS OF *AMPELISCA AGASSIZI* (JUDD) AND SOME OTHER GAMMARIDEANS

PHYLLIS T. JOHNSON[1]

ABSTRACT

Microsporidan infections were found in individuals of 11 species of benthic amphipods collected during a 2½-year survey of populations on the continental shelf of the northeastern United States. *Ampelisca agassizi* (Judd) was the most numerous and broadly distributed species of amphipod. A microsporidan confined to the abdominal muscles was common in most populations of *A. agassizi*. It is provisionally assigned to the genus *Thelohania*. There were prevalences up to 37% depending upon the population surveyed, but the microsporidans did not seem to contribute to mortality in *A. agassizi* populations, with the possible exception of adult males. Microsporidans in other amphipod species parasitized various organs and tissues according to the amphipod species and type of microsporidan. The relationships of the microsporidans with the genera *Thelohania*, *Stempellia*, and *Nosema* are discussed.

In the late 1970's, a monitoring program was developed within the National Oceanic and Atmospheric Administration (NOAA) to assess the presence of pollutants and their effects on the fauna and flora of the continental shelf of the United States. As a part of this plan, the Northeast Monitoring Program (NEMP) has been conducted on a seasonal basis from the Gulf of Maine to Cape Hatteras by the Northeast Fisheries Center, National Marine Fisheries Service. In connection with NEMP, studies have been made of types and prevalences of parasites, diseases, and other abnormalities of various populations of benthic gammaridean amphipods. Samples were mainly from stations on the Georges Bank and Mid-Atlantic Bight.

The results of the survey will be presented in a series of papers. This, the first report, discusses microsporidan parasites, particularly those of *Ampelisca agassizi* (Judd).

Published information on parasites and pathological conditions of gammaridean amphipods is limited and concerns mainly the parasites of selected estuarine and freshwater species, particularly the microsporidan parasites (Bulnheim 1975). Data collected during the present survey concern a broad array of species of marine amphipods. Communities of benthic amphipods are unlike most animal communities because they are composed of numerous individuals of several to many related species that live in very close proximity to one another. Indeed, it is common for a population to contain two or more species of a single genus. It is also common for a thousand or more individuals of a single species, together with varying numbers of other species, to be crowded onto one-tenth of a square meter of the bottom (Dickinson et al. 1980). This unique population structure makes studies of parasites and diseases of the amphipods of great general biological interest.

The methods used for collecting and preparing the benthic amphipods are satisfactory for study of many facets of the host-parasite relationships that exist in these animal communities: effects of parasites on their hosts, host specificity of parasites, seasonal prevalence, and modes of passage of parasites through host populations. On the other hand, paraffin-embedded sections seldom allow specific identification of parasites. Depending on the parasite group, this may require examination of live animals or of whole specimens fixed and stained by special methods.

It is hoped that the data presented here and elsewhere will serve as a framework for more definitive studies on the taxonomy, life history, and other aspects of the various parasite species.

MATERIALS AND METHODS

Amphipods were sampled 11 times over a 2½-yr period from July 1980 to December 1982 on NEMP cruises (Table 1). The 35 stations where benthic amphipods were collected are shown in Figure 1. Not all stations were visited on each cruise, being sampled from 1 to 10 times each during the survey. The 11 stations indicated by solid circles on Figure 1 had

[1]Northeast Fisheries Center, Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654.

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TABLE 1.—Sampling cruises for benthic amphipods, July 1980-December 1982.

Date	NEMP cruise no.	Cruise designation
July 1980	AL80-07	A
September 1980	AL80-09	B
December 1980	DE80-09	C
April-May 1981	KE81-04	D
July 1981	AL81-07	E
August-September 1981	AL81-10	F
November 1981	DE81-07	G
January-February 1982	AL82-01	H
March-April 1982	AL82-03	I
August-September 1982	AL82-10	J
November-December 1982	AL82-12	K

consistent, and usually numerous, amphipod populations and were sampled five or more times. They yielded the majority of data presented in this paper.

Collections of bottom sediments and accompanying biota were made with a 0.1 m^2 Smith-McIntyre[2] grab. Generally a single grab was taken at each station sampled. If the first grab contained few amphipods but was from a station where they usually were abundant, a second and sometimes a third grab was taken. Sediment contained in the grab was washed through a 1.0 mm sieve, and amphipods were either collected with forceps or gently scraped from the sieve and placed in a jar of 10% seawater Formalin. On cruises A, B, and E (see Table 1), supplemental specimens were collected at some stations by use of an epibenthic sled or scallop dredge.

Storage of samples was in Formalin except that amphipods were transferred temporarily into 30 ppt artificial seawater for identification and enumeration, inspection for various gross lesions, and for determination of life-history stages and microsporidan infections of the muscle in the case of *Ampelisca agassizi* (Judd). A stereomicroscope was used for these procedures. Up to 30 and occasionally more individuals of each species in the sample, depending on numbers present, were processed for histological examination by standard means. Finished tissue sections were stained with hematoxylin and eosin. Depending on size and number to be embedded, 1 to 12 amphipods of a single species from a single station were embedded on their sides in each paraffin block. Several serial sagittal sections were taken, first laterally and then near the midline of the amphipods. Because of unavoidable variations in size and depth of the amphipods in the block, not all were sectioned at the same levels. Parts of the hemocoel, skeletal muscle, and appendages of all amphipods were present in sections. Usually, parts of the gills, hepatopancreas and other parts of the gut, heart, brain, and gonads were also present. Other tissues and organs, particularly the antennal gland, hemopoietic tissues, eyes, and ventral nerve cord, often were not included.

Measurements of microsporidan spores were based on fixed material, either whole or embedded, sectioned, and stained.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The amphipod population sampled at any one time at a particular station was a mixture of up to 14 different species. Commonly five to eight species were collected in a single grab except at station 23, which was strongly dominated by *Ampelisca agassizi*. Of eight samples from station 23, three contained only *A. agassizi*, and *A. agassizi* made up 94 to 99% of the remaining samples. Totals of the eight samples from station 23 were 2,788 individuals of *A. agassizi* and 23 individuals of other species (99% *A. agassizi*).

Ampelisca agassizi was the most numerous and broadly distributed of the species investigated, and occurred at 17 stations including the 11 major ones. Certain information on the life history of this species is pertinent. It is an annual, tube-building species that produces a single brood of young (Bousfield 1973). Overwintering is in the juvenile stage. Gonads of both sexes develop during the subadult stage. Breeding begins in the spring, and newly ovigerous females are found from spring through autumn. Postovigerous females tend to remain in the population for an unknown period after the young are released from the brood pouch. Adult males are pelagic or epibenthic, probably short-lived, and usually were missing from samples collected with the Smith-McIntyre grab. Only the adult male has strongly developed transverse pleosomal muscles (muscles of the first three abdominal segments) (Fig. 2). Presumably, these muscles aid in swimming. The transverse muscles lie lateral to the longitudinal muscles and are developed during the subadult stage. They can be seen in various stages of development through the translucent cuticle of subadult males.

Females of the gammaridean, tube-dwelling amphipods so far studied leave their tubes to molt to the adult stage. Mating and egg extrusion take place in the water column (Mills 1967). Population dispersal is presumed to occur either by ovigerous females settling away from their original location

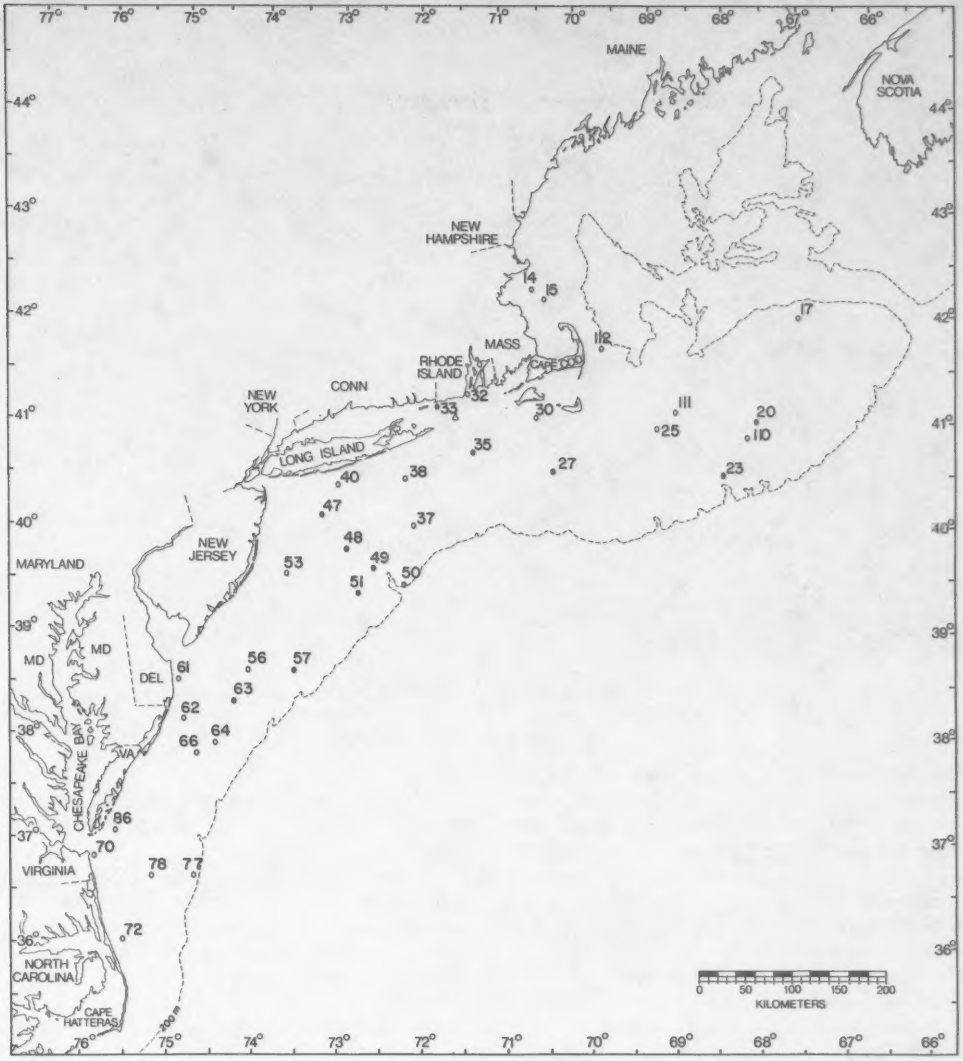

FIGURE 1.—Benthic stations of Northeast Monitoring Program at which populations of gammaridean amphipods were sampled during the survey, 1980-82.

and probably in a less populated area (Mills 1967) or by emigrating juveniles (Bousfield 1973). Thus, juveniles and perhaps ovigerous and postovigerous females of *A. agassizi* and other species could at times be immigrants into locations with already established populations of older juveniles and subadult males and females.

Microsporidans of *Ampelisca agassizi*

Most of the populations of *A. agassizi* sampled were regularly infected by a species of microsporidan that attacks the longitudinal pleosomal muscles (Figs. 3, 4). Infected muscles were chalky white in fully developed infection, and easily visible through

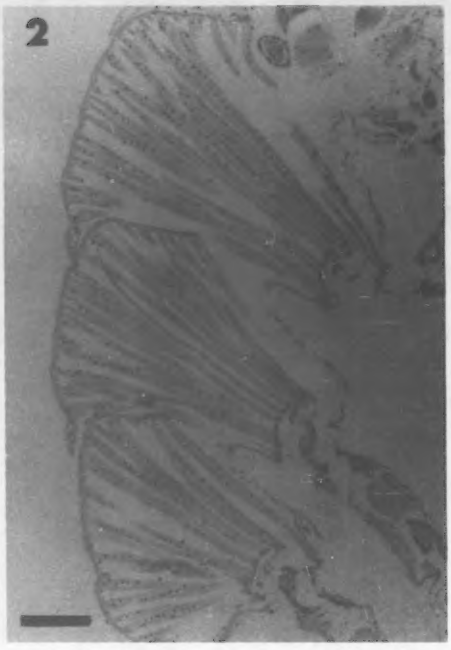

FIGURE 2.—*Ampelisca agassizi*: Transverse pleosomal muscles of an adult male. Bar = 0.2 mm.

FIGURE 3.—*Ampelisca agassizi*: Longitudinal pleosomal muscles infected by microsporidans (open arrows). Normal muscle is also present (closed arrow). g, midgut. Bar = 0.2 mm.

the translucent cuticle. Usually, only one to three muscles were infected. Inspection of 150 microsporidan-infected amphipods showed that in eight cases transverse pleosomal muscles were also involved, and in three cases, only the transverse muscles were infected. One postovigerous female, with microsporidan infection in muscle, also had what appeared to be the same organism in one of the ganglia of the ventral nerve cord.

On the basis of a tissue section she examined, A. Cali[3] determined that this microsporidan is a pansporoblastic organism with the clusters appearing to be in groups of eight. However, she said further that possibly some clusters contained more than eight spores. This is a point difficult to determine in sectioned material. Spores are oval and of fairly uniform size. Ones dissected out singly from infected muscle (not paraffin embedded) measured approximately 3 μm × 1.5 μm. In Cali's opinion, the *A. agassizi* parasite is best provisionally placed in the genus *Thelohania*, without specific designation.

[3]A. Cali, Rutgers University, Newark, NJ 07102, pers. commun. 1983.

Numerical information on this microsporidan is based on samples taken on cruises D-K, because determination of microsporidan infection was by study of sectioned material only from cruises A-C, and infections can be missed by this method. Considering all stations on cruises D-K, juveniles had a lower prevalence of grossly visible infection than did male and female subadults and ovigerous females (Table 2), but this was not invariably the case in individual samples. In 5 of the 38 samples with micro-

TABLE 2.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. All stations, cruises D-K.

Life-history stage	No. infections/ total collected (% prevalence)
Juveniles	517/4,868 (11)
Subadults	1,335/5,293 (25)
Ovigerous females	111/501 (22)
Postovigerous females	82/413 (20)
Adult males	1/55 (2)
Totals	2,046/11,130 (18)

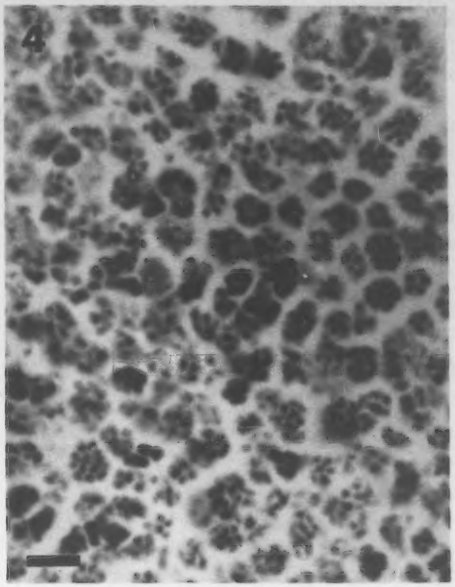

FIGURE 4.—*Ampelisca agassizi*: Groups of spores and prespores of the muscle-infecting microsporidan. Bar = 10 μm.

sporidan-infected *A. agassizi*, prevalence was equal to or slightly higher in juveniles than in subadults or ovigerous females. Prevalence was very low in the small sample of adult males, but varied considerably in individual samples of both males and postovigerous females (Table 3). The three stations with the most consistently numerous populations of *A. agassizi* also had the highest prevalences of microsporidan infection. These were stations 23, 33, and 48, with overall prevalences of 30%, 37%, and 22%, respectively. Overall prevalence at other stations ranged from 0 to 14%.

The majority of infected hosts showed no reaction to the presence of the microsporidans. However, there was occasional melanization in heavily infected muscle, with invasion of hemocytes into the mass of spores, some encapsulation of spores and infected muscle, and lysis of many spores. In these cases, it appeared that the muscle had lost its integrity; that is, the sarcolemma probably was no longer entire. Often, other infected muscle near the necrotic mass of spores and muscle showed no evidence of attack by host defense mechanisms.

The second microsporidan of *A. agassizi* parasitized epithelial cells of the posterior half of the midgut. Juveniles, male and female subadults, and ovigerous and postovigerous females were infected. The parasite resembled *Nosema*, the spores being single and free in the cytoplasm of the host cell (Fig. 5). Spores were slightly oval and about 2 μm in the greater dimension. Infected cells were hypertrophied (Fig. 6). In one heavy infection, many spores were free in the gut and apparently most infected cells had ruptured. There was no host reaction to infection. This parasite occurred twice in individuals with microsporidan infection in abdominal muscle. Based on sectioned material, overall prevalence of the gut microsporidan was < 0.1% (25/2403). Prevalence in samples with one or more infected *A. agassizi* was 3.7% (25/678), range 1-6%. Amphipods with microsporidans in the gut epithelium were from stations 23, 33, 47, 48, 49, 50, and 51.

Microsporidans in Species Other Than *A. agassizi*

Males and females of *Unciola* species (probably all *U. irrorata* Say and *U. inermis* Shoemaker) were hosts to a microsporidan that infected longitudinal muscles of the pleosome. In three instances, a similar or the same microsporidan was found in a ganglion of the ventral nerve cord, and not in muscle. Spores appeared similar to those of the *A. agassizi* parasite; they measured about 3 × 1.5 μm; and there were eight or more spores per envelope. Unlike the *A. agassizi* parasite, vegetative stages were often present along with developed and developing spores. *Unciola* species have an opaque cuticle, and infected muscle cannot be seen grossly. Based on sectioned

TABLE 3.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. Stations 47 and 48, cruises E and F.

Life-history stage	No. infections/ total collected (% prevalence)	No. infections/ total collected (% prevalence)
	Cruise E	Cruise F
Station 47	(depth 48 m)	(depth 62 m)
Juveniles	29/851 (3)	130/1,124 (12)
Subadults	45/258 (17)	12/53 (23)
Ovigerous females	14/84 (17)	11/53 (20)
Postovigerous females	0/24 (0)	6/29 (21)
Adult males	0/34 (0)	1/3 (33)
Totals	88/1,251 (7)	160/1,262 (13)
	Cruise E	Cruise F
Station 48	(depth 72 m)	(depth 68 m)
Juveniles	2/33 (6)	5/29 (17)
Subadults	66/246 (27)	28/111 (25)
Ovigerous females	0 (—)	11/51 (22)
Postovigerous females	0 (—)	3/27 (11)
Adult males	0/1 (0)	0/4 (0)
Totals	68/280 (24)	47/222 (21)

FIGURE 5.—*Ampelisca agassizi*: *Nosema*-like microsporidan in the midgut epithelium. Bar = 10 μm.

FIGURE 6.—*Ampelisca agassizi*: Hypertrophy of midgut epithelial cells infected by a *Nosema*-like microsporidan. Infected epithelium to left, normal epithelium to right. Bar = 60 μm.

material, prevalence was 8.3% (23/277), considering only samples containing infected *Unciola* spp. Prevalence was 1.7% when considering all *Unciola* spp. that were sectioned and examined (Table 4). There was no host reaction to infection in the ganglia, but animals with muscle infection often showed some melanization and encapsulative response (Fig. 7). Scattered small melanized nodules were common in the hemocoel of infected *Unciola* spp., but it was not evident whether they had formed in response to microsporidans.

Other amphipod species with microsporidan infections are listed in Table 4. Prevalence was usually very low. Most of the parasites appeared like the muscle-infecting microsporidans of *A. agassizi* and *Unciola* spp. A *Nosema*-like parasite similar to the gut microsporidan of *A. agassizi*, but smaller (0.7 μm), occurred in the hepatopancreatic epithelium of a specimen of *Leptocheirus pinguis* (Stimpson). Another *L. pinguis* harbored a larger *Nosema*-like species in oocytes and heart muscle. Infected oocytes were necrotic and encapsulated by hemocytes. The generalized muscle parasite of *Melita dentata* (Krøyer) *s. lat.* was also *Nosema*-like.

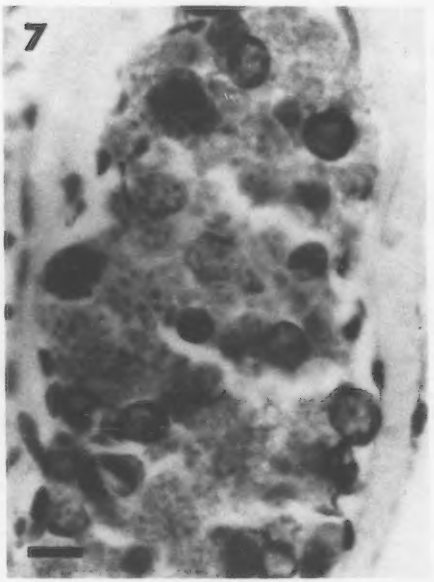

FIGURE 7.—*Unciola* sp.: Host reaction to microsporidans in abdominal muscle. Some groups of degenerating spores and prespores are surrounded by melanized material. A few nuclei of encapsulating host cells are visible around the mass of microsporidans. Bar = 10 μm.

TABLE 4.—Microsporidans in amphipods other than *Ampelisca agassizi*.

Amphipod species	No. infections/ total examined (% prevalence)	Positive stations	Tissues infected	Type of microsporidan
Unciola spp. (*irrorata* Say and *inermis* Shoemaker)	23/1,365 (1.7)	33, 35, 38, 47, 48, 51, 110, 112	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"
Ampelisca vadorum Mills	4/448 (0.9)	57, 66	Muscle, tegmental glands, oocytes	"*Thelohania*"
Ampelisca verrilli Mills	1/48 (2.1)	62	Connective tissue, muscle	"*Thelohania*"
Ericthonius rubricornis Smith	1/436 (0.2)	38	Abdominal muscle	"*Thelohania*"
Eriopisa elongata (Bruzelius)	1/29 (3.4)	47	Ganglia of ventral nerve cord	"*Thelohania*"
Leptocheirus pinguis (Stimpson)	1/913 (0.1)	47	Abdominal muscle	"*Thelohania*"
	1/913 (0.1)	15	Oocytes, heart muscle	*Nosema*-like
	1/913 (0.1)	20	Epithelium of hepatopancreas	*Nosema*-like
Melita dentata (Krøyer) *s. lat.*	2/44 (4.5)	51	Generalized in muscle	*Nosema*-like
Monoculodes edwardsi Holmes	1/110 (0.9)	40	Abdominal muscle	"*Thelohania*"
Photis dentata Shoemaker	4/301 (1.3)	33	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"

The microsporidan of *Ampelisca vadorum* Mills resembled that of *Unciola* spp., but fully developed spores were not seen (Fig. 8). Muscle, tegmental glands, and oocytes were infected. Often, groups of microsporidans had "used up" the host tissue, and appeared like groups of extracellular, closely knit, vegetative and sporulating stages, but some of these groups were unmistakably in the shape of tegmental glands and oocytes and were in the correct anatomical positions. In one case, muscle fibers were still present adjacent to the mass of microsporidans and in another, microsporidans infected a recognizable tegmental gland. Host reactions to the microsporidans had not occurred in the few infected *A. vadorum* available for study.

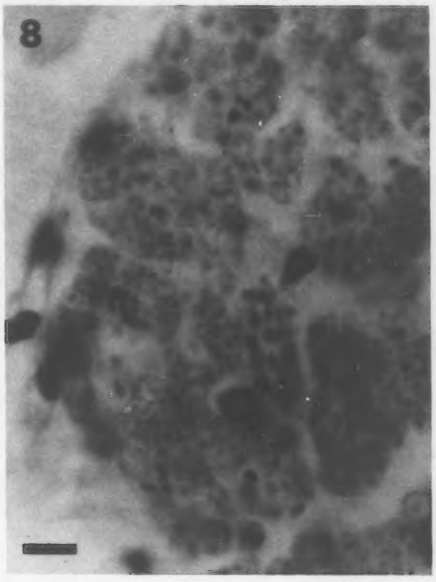

FIGURE 8.—*Ampelisca vadorum*: Vegetative and prespore stages of a muscle-infecting microsporidan. Bar = 10 μm

More than 35 specimens each of the following species were sectioned and examined, but microsporidans were not found: *Anonyx sarsi* Steel & Brunel (36 specimens), *Byblis serrata* Smith (316 specimens), *Casco bigelowi* (Blake) (60 specimens), *Corophium crassicorne* (Bruzelius) (50 specimens), *Harpinia propinqua* Sars (116 specimens), *Orchomenella minuta* Krøyer (64 specimens), *Phoxocephalus holbolli* Krøyer (73 specimens), *Pseudunicola obliquua* (Shoemaker) (46 specimens), and *Rhepoxynius epistomus* (Shoemaker) (249 specimens).

DISCUSSION

Bulnheim (1975) and Sprague (1977) have listed and discussed the various microsporidans reported from amphipods. Most of the hosts are freshwater and estuarine forms, and depending on the species

of microsporidan, muscles, ovaries, connective tissues, and gut epithelia are infected. One of the microsporidans, a parasite of *Gammarus pulex* L., infects the longitudinal abdominal muscles of its host in the same manner as does the *A. agassizi* parasite, but is known to have a variable number of spores per envelope. It was named *Glugea muelleri* (Pfeiffer, 1895, in van Ryckeghem 1930), later named *Thelohania giraudi* (Léger and Hesse, 1917), and has been called *Stempellia muelleri* (Pfeiffer) by Bulnheim (1975) and *Microsporidium giraudi* (Léger and Hesse) by Sprague (1977). The relationship of "*Glugea muelleri* Pfeiffer" and the microsporidan from *A. agassizi* remains to be determined. Although "*Glugea muelleri* Pfeiffer" and the *A. agassizi* parasite are remarkably similar in being restricted to the longitudinal abdominal muscles of their hosts, the latter is probably significantly smaller. Fixed spores of the *A. agassizi* parasite are about 1.5 × 3 μm, and fresh spores of "*Glugea muelleri*" are 2.2 × 4.5 μm.

The method of transmission of the *A. agassizi* parasite is not known. Microsporidans are usually transmitted orally, but transovarial transmission also occurs in amphipods. Transovarially transmitted microsporidans of *Gammarus duebeni* Lilljeborg infect the ovary, and, depending on the species, cause complete or partial feminization of males (Bulnheim 1975, 1977). The parasite of *A. agassizi* did not infect the ovary, and because it was regularly found in normal males, it apparently does not cause feminization of males. Bulnheim (1971) successfully transmitted "*G. muelleri* Pfeiffer" to several species of *Gammarus*, including euryhaline ones, by feeding of infected muscle.

Prevalence of the muscle parasite of *A. agassizi* apparently increases with age of the host, and it could be hypothesized that this microsporidan is transmitted orally, that the older the host the more chances it has had to become infected, and that the parasite does not contribute to increased mortality in the population. Adult males are active swimmers and might prove an exception because impaired muscle function could lead to increased predation. If this occurred, one would expect infected males to be preferentially removed from the population, leading to a lower prevalence of infection in this stage. Indeed, prevalence in adult males was only 2%. However, relatively few males were collected during the survey, and the low prevalence could prove to be sampling artifact. Note that in the sample from cruise E, station 47 (Table 3), both postovigerous females and adult males were uninfected, but 2 mo later, at the same station, prevalence in postovigerous females was 21% and the only infected adult male found during the survey was also collected at that time. The discrepancy in prevalence might be due to sampling of slightly different populations. As discussed below, there is no assurance that the same population was sampled spatially, and temporal differences conceivably might also have complicated the results.

Relationships of the microsporidans seen in the various species of amphipods could not be decided on the basis of material fixed and prepared as it was. It would be interesting to determine whether the parasites of *Unciola* spp. and *Ampelisca vadorum* are the same or different species, and what their relationship is to the *A. agassizi* parasite. There were some differences in the habits and the developmental stages present in the three amphipods. Vegetative stages were common in the case of the *A. vadorum* parasite and fairly common in *Unciola* spp., but usually rare or absent in *A. agassizi*. Several different tissues were infected in *A. vadorum*, but excepting a few infections in nervous tissue, only abdominal muscle was infected in *Unciola* spp. and *A. agassizi*. Previous investigators have found that microsporidan infection is well tolerated by amphipod hosts, and that defense reactions against these parasites generally are limited and may come into play mainly when host tissue becomes necrotic (reviewed by Bulnheim 1975). The muscle-inhabiting microsporidan of *A. agassizi* is obviously a primary parasite of that species and is seldom attacked by the host. However, the similar parasite of *Unciola* spp. often either provokes attack merely by its presence or damages the muscle so that a response occurs to the necrotic tissue. In either event, it is possible that this parasite is not fully adapted to *Unciola* spp., because arthropods are known to be less tolerant of non-adapted parasites (Salt 1970; Unestam and Weiss 1970)

With exception of the muscle-infecting species from *A. agassizi*, microsporidans are not common parasites of benthic amphipods in the areas sampled, even considering that some infections must have been missed because not all would be seen in the limited number of sections examined from each amphipod.

Sampling methods used in the survey do not lend themselves to precise studies on progression of parasitic infections through particular populations. Sampling cannot be done often enough to show if and when additions to populations (with perhaps different prevalences of parasites) are provided by immigrating juveniles or other stages of these short-lived animals. Further, populations may not be

homogeneous over the area sampled at a single station. Sediment sampling with a grab is imprecise, as the different depths of samples taken at stations 47 and 48 on cruises E and F testify (Table 3). It is probable that return to an exact location was never accomplished. Even if populations were homogeneous, predation by fish, and other short-term disturbances, may cause local impoverishment of populations or differences in population composition that would not be detected in the necessarily blind sampling done with a Smith-McIntyre grab.

A general pattern does emerge. In the area surveyed, microsporidans are dominant parasites of the most numerous and ubiquitous species, *A. agassizi*, but are rare in all other species. This may be a reflection of the fact that only *A. agassizi* consistently occurred in dense populations at certain stations at all sampling times, a circumstance that would promote spread of a host-specific and horizontally transmitted parasite.

ACKNOWLEDGMENTS

Thanks are due to Frank Steimle and Robert Reid of the Northeast Fisheries Center Sandy Hook Laboratory, and Linda Dorigatti, Gretchen Roe, and Sharon MacLean of the Oxford Laboratory, who collected the amphipods. Ann Frame, Sandy Hook Laboratory, provided expert advice and training in identification of amphipods. Linda Dorigatti identified material from cruises A-C, and along with Gretchen Roe, Dorothy Howard, and Cecelia Smith of the Histology Section, Oxford Laboratory, prepared the specimens for histological examination. Ann Cali, Rutgers University, Newark, NJ, reviewed the manuscript and provided identification of the muscle-inhabiting microsporidan of *A. agassizi*.

LITERATURE CITED

BOUSFIELD, E. L.
1973. Shallow-water Gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, N.Y., 312 p.

BULNHEIM, H.-P.
1971. Über den Wirtskreis der Mikrosporidie *Stempellia mülleri*. Arch. Protistenkd. 113:137-145.
1975. Microsporidian infections of amphipods with special reference to host-parasite relationships: a review. Mar. Fish. Rev. 37(5-6):39-45.
1977. Geschlechtsumstimmung bei *Gammarus duebeni* (Crustacea, Amphipoda) unter dem Einfluss hormonaler und parasitärer Faktoren. Biol. Zentralbl. 96:61-78.

DICKINSON, J. J., R. L. WIGLEY, R. D. BRODEUR, AND S. BROWN-LEGER.
1980. Distribution of gammaridean Amphipoda (Crustacea) in the Middle Atlantic Bight region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-741, 46 p.

LÉGER, L., AND E. HESSE.
1917. Sur les Microsporidies de la Crevette d'eau douce. C. R. Seances Soc. Biol. Fil. 80:12-15.

MILLS, E. L.
1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Board Can. 24:305-355.

SALT, G.
1970. The cellular defence reactions of insects. Cambridge Univ. Press, Cambridge, 118 p.

SPRAGUE, V.
1977. Systematics of the Microsporidia. *In* L. A. Bulla, Jr., and T. C. Cheng (editors), Comparative pathobiology, Vol. 2. Plenum Press, N.Y., 510 p.

UNESTAM, T., AND D. W. WEISS.
1970. The host-parasite relationship between freshwater crayfish and the crayfish disease fungus *Aphanomyces astaci*: responses to infection by a susceptible and a resistant species. J. Gen. Microbiol. 60:77-90.

VAN RYCKEGHEM, J.
1930. Les Cnidosporidies et autres parasites du *Gammarus pulex*. La Cellule 39:401-416.

LONG-TERM RESPONSES OF THE DEMERSAL FISH ASSEMBLAGES OF GEORGES BANK

WILLIAM J. OVERHOLTZ[1] AND ALBERT V. TYLER[2]

ABSTRACT

The resilience of demersal fish assemblages on Georges Bank was investigated with data from seasonal bottom trawl surveys conducted by the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Massachusetts, from 1963 to 1978. Cluster analysis proved to be a useful statistical method for delineating assemblage boundaries and associated species. Assemblages persisted over the long-term and changed spatial configuration only slightly on a seasonal basis. Declines in biomass, numerical density, and changes in relative abundance occurred ranging from mild to severe. Assemblage changes were probably triggered by intense fisheries as well as inherent trophic dynamics of component species. Results have useful multispecies management connotations. The assemblage concept appears to be an appropriate operational or conceptual framework for further management and modeling applications.

Most community ecological studies have necessarily concentrated on the short-term aspects or seasonality of assemblages. Typically 1 to 3 yr of field measurements are analyzed with information theory, niche breadth procedures, or multivariate statistical methods. Demersal fish assemblages in particular have been investigated in a number of locations [see studies by Tyler (1971), Oviat and Nixon (1973), Stephenson and Dredge (1976), Hoff and Ibara (1977), Gabriel and Tyler (1980), and Inglesias (1981)]. The recurrent theme in most of these studies centers around seasonally varying diversity because of environmentally induced migration, temperature usually acting as the dominant driving variable.

Unfortunately, many interesting questions cannot be addressed in these studies because of their short-term horizon. It is important to consider the long-term ramifications of fishery system responses. The temporal scale referred to here as "long-term" does not refer to geologic time, but rather ecological time, the span of years during which the actions of fishery ecologists evoke system responses. Fishery ecologists are limited in their ability to function within this time frame. For instance, a plant ecologist could predict with some certainty the type of forest that would eventually occupy a cleared site, if left undisturbed, but comparable knowledge for fishery systems is lacking, especially in the marine environment.

Are fish assemblages stable? How do they respond to exploitation? Holling (1973) investigated system responses to man's activities, showing that in closed systems, such as freshwater lakes, the propensity to remain stable is high, but not infallible. Smith (1972) critiqued the Great Lakes experience, concluding that the activities of man, notably fishing and pollution, when coupled with biological interactions, caused significant community alterations in this system. Few marine studies, with the exception of Soutar and Isaacs (1969), Sutherland (1980), DeVries and Pearcy (1982), and some general overview papers (Brown et al. 1976; Richards et al. 1978), have stressed the long-term temporal and spatial aspects of marine system response.

Longer term temporal and spatial questions were examined with data from research conducted at the Northeast Fisheries Center (NEFC) (Grosslein 1969). Concentrating on Georges Bank, we used cluster analysis to produce yearly fall and spring dendrograms for the period 1963-78 and 1968-78, respectively. Assemblages were defined, component species were identified, distributional maps plotted, and the information was examined to elucidate long-term temporal and spatial patterns. Further analyses led to trajectories of species catch-per-unit-effort (CPUE), assemblage total biomass, estimates of intra-assemblage diversity, and other measures of community response. It is suggested that fishing, coupled with interspecific interactions, appeared to have played a major role in determining trends in the Georges Bank assemblages.

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METHODS

Georges Bank, a large, submerged, marine plateau, is located off the northeastern coast of the United States (Fig. 1). It has been the site of an intense fishery for several centuries, and a large international fleet exploited the area from the 1960's to the mid-1970's. The NEFC has conducted annual bottom trawl surveys on the Northwest Atlantic continental shelf since the autumn of 1963. Annual spring surveys commenced in 1968 and, in addition, several summer and winter cruises have been undertaken on an intermittent basis. Surveys were conducted from Nova Scotia to Hudson Canyon from 1963 to 1966 and coverage was extended to Cape Hatteras beginning in 1967. Grosslein (1969) and Azarovitz (1982) described the details and justification for the surveys, but a brief summary is appropriate.

The objective of the surveys is to obtain statistically meaningful abundance estimates of the offshore marine fish populations in the aforementioned areas. Secondary objectives included the collection of data for distribution studies, age and growth determinations, predator-prey interactions, and a host of special purpose investigations. The potential area was divided into zones (strata) based on depth and biological considerations. Stratified random samples were selected with allocation to each strata proportional to its area. A 30-min sample with a standardized research bottom trawl and a 1.25 cm cod end liner was accomplished. All fish, as well as major invertebrates, were sorted to species, weighed, and measured, and some fish were sampled for other

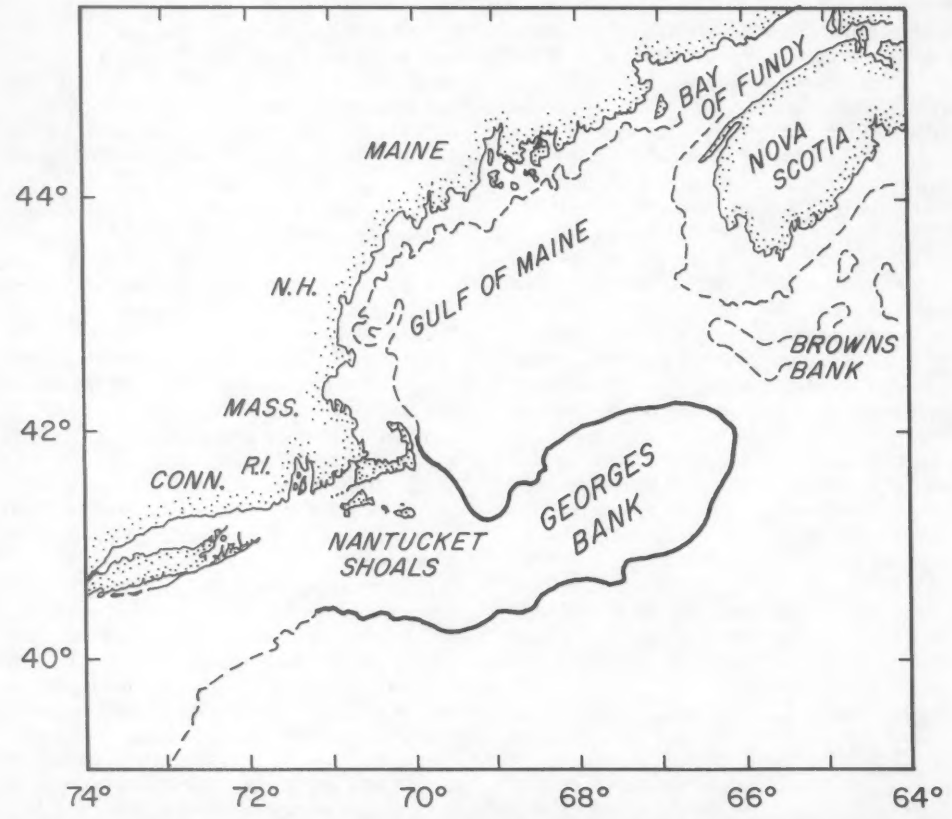


FIGURE 1.—Georges Bank and Gulf of Maine region with shoreline place names and other associated geographical landmarks.

analyses. Sampling frequency averages about one station for every 250 mi² or roughly 300 locations in a normal survey from Cape Hatteras to Nova Scotia.

Data from a selected portion of this time series was used in cluster analyses that defined demersal fish assemblages. Specifically, a group of 36 species representing the dominant fishes on Georges Bank, were chosen as the focus for the investigation (Table 1). This choice was based on a preliminary examination of the data to determine which species were most important in terms of biomass and numerical density. Catches (kg) for each of the species from every station in a particular cruise were organized into a data matrix and processed with an agglomerative cluster analysis program (Keniston 1978). To remove skewness in the species matrices, we transformed the data prior to clustering by using an ln $(x + 1)$ conversion. Station dissimilarities were calculated by using the Bray-Curtis dissimilarity index, an ecological distance measure that is sensitive to dominant species (Clifford and Stephenson 1975; Boesch and Swartz 1977).

TABLE 1.—Species cited by common name in the text.

Common name	Scientific name
Spiny dogfish	*Squalus acanthias*
Winter skate	*Raja ocellata*
Little skate	*Raja erinacea*
Smooth skate	*Raja senta*
Thorny skate	*Raja radiata*
Atlantic herring	*Clupea harengus*
Alewife	*Alosa pseudoharengus*
Offshore hake	*Merluccius albidus*
Silver hake	*Merluccius bilinearis*
Atlantic cod	*Gadus morhua*
Haddock	*Melanogrammus aeglefinus*
Pollock	*Pollachius virens*
White hake	*Urophycis tenuis*
Red hake	*Urophycis chuss*
Cusk	*Brosme brosme*
American plaice	*Hippoglossoides platessoides*
Summer flounder	*Paralichthys dentatus*
Fourspot flounder	*Paralichthys oblongus*
Yellowtail flounder	*Limanda ferruginea*
Winter flounder	*Pseudopleuronectes americanus*
Witch flounder	*Glyptocephalus cynoglossus*
Windowpane	*Scophthalmus aquosus*
Gulf stream flounder	*Citharichthys arctifrons*
Atlantic mackerel	*Scomber scombrus*
Butterfish	*Peprilus triacanthus*
Bluefish	*Pomatomus saltatrix*
Blackbelly rosefish	*Helicolenus dactylopterus*
Longhorn sculpin	*Myoxocephalus octodecemspinosus*
Sea raven	*Hemitripterus americanus*
Cunner	*Tautogolabris adspersus*
American sand lance	*Ammodytes americanus*
Atlantic wolffish	*Anarhichas luptus*
Ocean pout	*Macrozoarces americanus*
American goosefish	*Lophius americanus*
Short-finned squid	*Illex illecebrosus*
Long-finned squid	*Loligo pealei*

The resulting dissimilarity matrix was used in a group average fusion strategy to combine stations with similar species distributions (Clifford and Stephenson 1975). These station combinations were displayed in dendrograms, which were examined and assemblage groups were chosen by two criteria: large-scale separations, as shown in Figure 2, and dissimilarity levels. Stations from these assemblage groups were plotted on cruise maps from the original sampling plan and areas were delineated. This process was repeated for all spring and fall cruises to provide a consecutive series of maps, which were then examined for continuity (Fig. 3). Finally, data from several consecutive years were pooled to delineate assemblages designated, based on nearby geographic features or depth zones.

Species lists were prepared for the assemblages outlined in the pooled cluster results, and data were analyzed to further define the structure of each group. Length frequencies from species in the different assemblages were used to separate life history stages and catch-per-tow data were used to investigate trends in distribution and abundance. Examination of food habit data in the literature and NEFC documents gave further insight into assemblage structure. Trajectories of assemblage CPUE for selected species were plotted and examined for long-term trends. Total assemblage CPUE was also investigated and compared with previous trends reported by other authors for the region.

Gradient analyses were performed with the objective of explaining species distributions based on a set of location, physical, and chemical variables. Canonical correlations, using information on latitude, longitude, depth, bottom temperature, bottom oxygen, and bottom salinity, were employed to define possible gradients that might be useful indicators of species distribution (Pimentel 1979). Data for the autumn cruise were obtained from measurements of bottom temperature and depth made aboard the RV *Albatross IV* (U.S.A.) 20 October to 5 November 1976, and corresponding information on bottom salinity and oxygen from the RV *Anton Dohrn* (Federal Republic of Germany) 14 November to 1 December 1976. Information for the spring cruise was procured from measurements of bottom temperature and depth from the RV *Albatross IV*, 17 April to 3 May 1978, and salinity and oxygen data that was obtained from the RV *Argus* (Union of Soviet Socialist Republics) from 13 to 28 April 1978; these two data sets were chosen because they corresponded closely in time to the available station information.

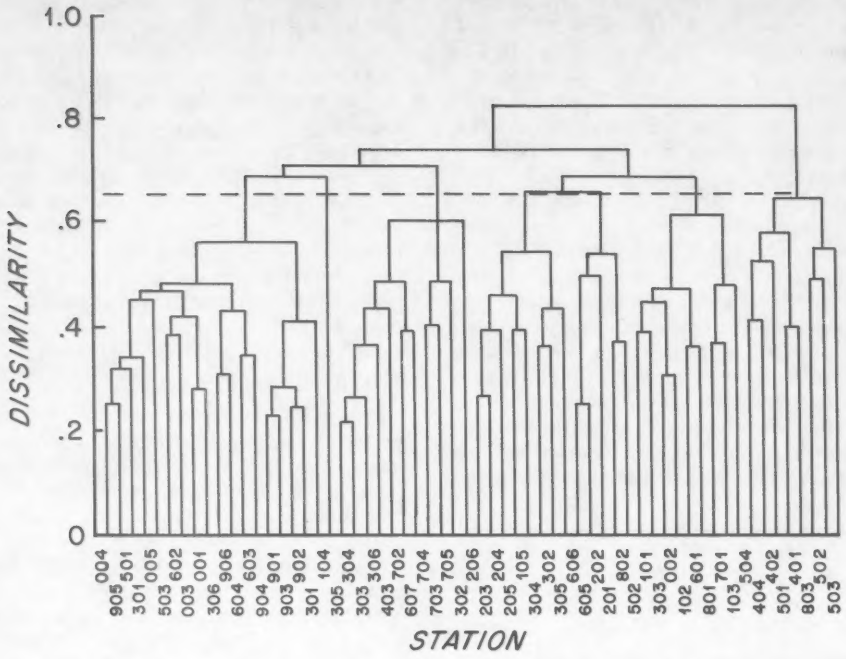


FIGURE 2.—Typical dendrogram, autumn 1966, showing cluster station groups and dissimilarities. Dashed line indicates a dissimilarity of 0.65.

RESULTS

Five important assemblage groups were present on Georges Bank from fall 1963 to 1978. For reference, we name these groups: Slope and Canyon, Intermediate, Shallow, Gulf of Maine Deep, and Northeast Peak. A consistent spatial pattern emerged as consecutive fall cruises were examined and plotted. The same five groups appear to have been present in similar locations since 1963. These five assemblages were present at the mid- and endpoints of the fall time series also (Fig. 3). The groups appear to change their spatial configuration slightly on an annual basis, but the general area of each group was maintained. Lists of the dominant species in each assemblage are given in Table 2.

The total area that each assemblage encompassed through time (years) was delineated by pooling the observations from consecutive years. Figure 4 shows an example of a representative assemblage from the spring and fall, respectively. The groups overlapped surprisingly little through time with the exception of a few border stations along adjacent assemblages.

TABLE 2.—Assemblage species associations from cluster results (demersal species only).

Slope and canyon:	Red hake
Silver hake	Summer flounder
White hake	Yellowtail flounder
Red hake	Winter flounder
Gulf stream flounder	Windowpane
Offshore hake	Longhorn sculpin
Fourspot flounder	Sea raven
Blackbelly rosefish	Ocean pout
American goosefish	Sand lance
Intermediate:	American goosefish
Winter skate	Gulf of Maine Deep:
Little skate	Thorny skates
Red hake	American plaice
Silver hake	Witch flounder
Atlantic cod	White hake
Haddock	Silver hake
Sea raven	Atlantic cod
American goosefish	Haddock
Ocean pout	Cusk
Longhorn sculpin	Atlantic wolffish
Yellowtail flounder	Northeast Peak:
Shallow:	Thorny skate
Winter skate	Atlantic cod
Little skate	Haddock
Silver hake	Pollock
Atlantic cod	White hake
Haddock	Winter flounder
Pollock	Ocean pout
White hake	Longhorn sculpin

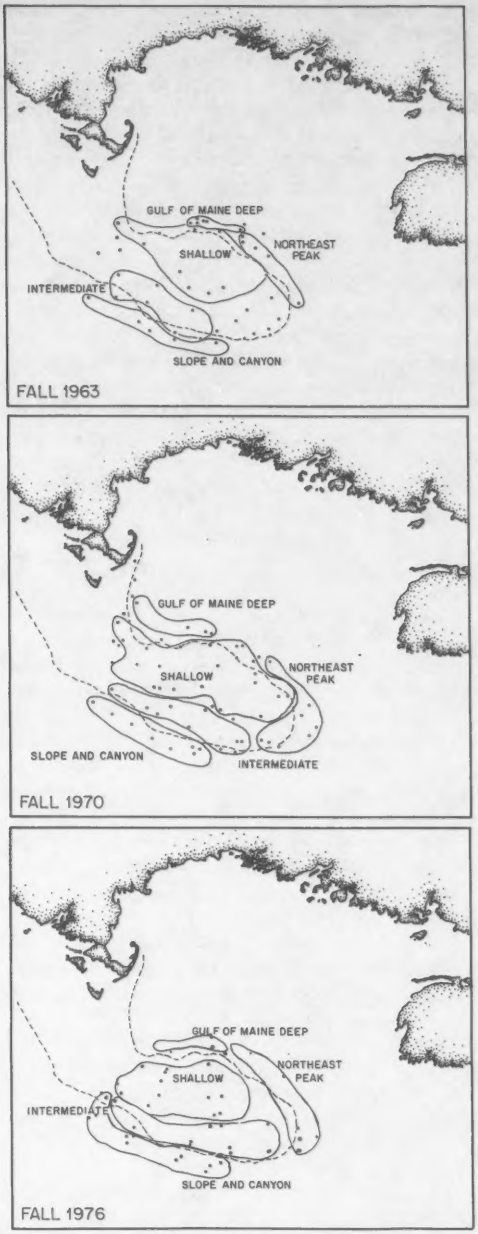


FIGURE 3.—Georges Bank assemblages for three autumn surveys 1963, 1970, 1976.

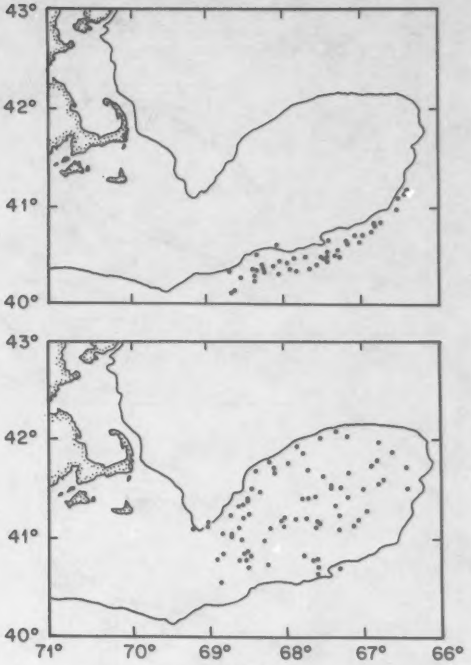


FIGURE 4.—Sample pooled station distributions for the Slope and Canyon assemblage, spring 1968-73 (top panel) and the Shallow assemblage, autumn 1963-67.

Data for all cruises were pooled by season and used to generate composite maps of general assemblage areas, for the spring and autumn (Fig. 5). The Slope and Canyon assemblage appears to encompass a similar area regardless of season, while some of the other assemblages changed slightly. The Shallow assemblage covered most of Georges Bank in the spring (Fig. 5) and was slightly smaller in the fall (Fig. 5). The Intermediate assemblage is somewhat larger in the fall (Fig. 5), suggesting a migration of the species in this area to shallower water as the year progresses. Assemblages in the spring appear to follow depth contours resulting in the elongate shape of the groups at this time (Fig. 5). The Northeast Peak Interior (NPI) and Northeast Peak-Gulf of Maine Deep (NPGM Deep) assemblages show definite seasonal spatial changes when compared with the Gulf of Maine Deep (GM Deep) and Northeast Peak assemblages in the fall (Fig. 5). The general shape and location of the fall assemblages suggests that a different set of oceanographic and biological forcing factors are important in deter-

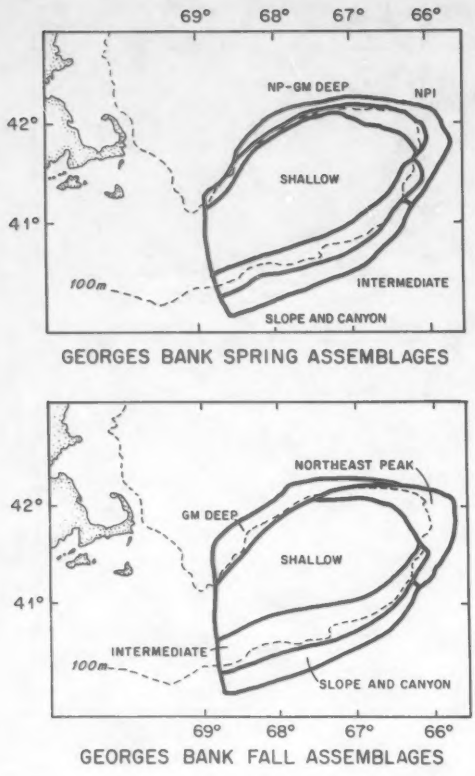


FIGURE 5.—Composite maps showing seasonal changes in the Georges Bank assemblages and their approximate areas. NPI = Northeast Peak Interior; NPGM Deep = Northeast Peak-Gulf of Maine Deep; GM Deep = Gulf of Maine Deep.

mining the distribution of fish. The Northeast Peak assemblage, for instance, spans several depth zones and encroaches on the Shallow assemblage, reducing its area during this part of the year.

The assemblage maps presented in Figure 5 were useful for organizing the 36 species of Table 1 into their corresponding demersal subunits (Table 2). Four basic species categories were defined in the various assemblages. These included ubiquitous species, resident species, periodics, and those resident species present in several assemblages during different parts of their life history. Ubiquitous species, such as ocean pout, goosefish, sea raven, and Atlantic cod, were found with regularity in almost all of the assemblages. Resident species, such as little skate, winter skate, longhorn sculpin, yellowtail flounder, winter flounder, American plaice, and witch founder, were present in only one or two assemblages in abundance. Periodic or seasonal migrants include bluefish, butterfish, and mackerel, as well as short-finned squid and long-finned squid. These species moved in and out of the various assemblages on a seasonal basis with temperature being a likely dominant force, and were often highly variable in terms of their abundance and were therefore not included in Table 2.

A number of species, including silver hake, red hake, white hake, and haddock, were present in more than one assemblage as different life history stages. Silver hake, for example, are found in the Slope and Canyon and Shallow assemblages, with adults on the average, occurring more frequently in the Slope and Canyon and Gulf of Maine Deep assemblage, while juveniles are more abundant in the Shallow assemblage. It appears that for many of the abundant fish species on Georges Bank, adults occupy the deeper peripheral assemblages while juveniles of these same species occupy the shallower zones during much of the year.

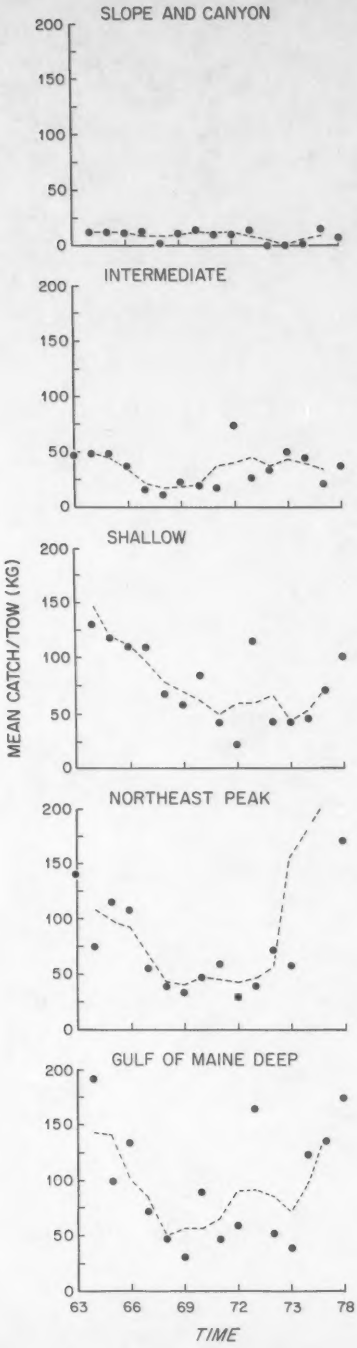
ASSEMBLAGE TRAJECTORIES

Assemblage CPUE indices were calculated for several of the spring and fall assemblages and used for evaluating temporal trends in total catch and catch by species. Assemblage CPUE declined dramatically in the mid-1960's to early 1970's in four of five Georges Bank assemblages in fall (Fig. 6). In particular, research catches in the Shallow, Northeast Peak, and Gulf of Maine Deep assemblages reached all-time lows in the early 1970's, coincident with large increases in international effort and landings at that time (Figs. 6, 7). International effort, measured in thousands of days fished, increased threefold over the period 1960-69 (Fig. 7). Assemblage biomass showed some signs of recovery in the late 1970's when good year classes of Atlantic cod, haddock, and other species occurred and international effort declined due to the Magnuson Fishery Conservation and Management Act of 1976 (Figs. 6, 7).

Research catch of silver hake, fourspot flounder, red hake, white hake, and black belly rosefish remained nearly stable over the spring period (1968-75), then increased abruptly after 1976 due to increases in the silver hake (Fig. 8A).

Total catch for the fall time series was also stable for most years, until 1972 when silver hake and red hake abundance fluctuated (Fig. 8B).

Figure 8C shows the trends in percent by weight for the five species during fall indicating a change in biomass dominance for silver hake and red hake. Blackbelly rosefish and fourspot flounder showed the



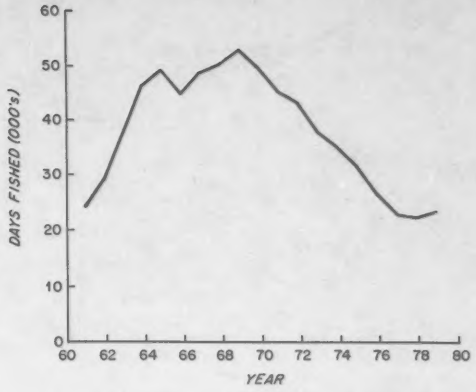


FIGURE 7.—Unstandardized effort data in thousands of days fished for the Georges Bank demersal fishery, all countries, for 1961-79, expressed as 3-yr moving means.

same trends as in the former case, but represented more of the catch on a percent weight basis in the later years of the fall time series (Fig. 8C). Gulf Stream flounder was actually one of the more important species numerically during the mid-years of the series (Fig. 8D). The same general trend for red and silver hake, and the other species is apparent in the percent by numbers data (Fig. 8D).

The shallow assemblage was much more diverse than the Slope and Canyon assemblage. The major species of importance were Atlantic cod, winter skate, longhorn sculpin, little skate, yellowtail flounder, and haddock. Mean catch per tow in the fall time series declined dramatically from 202 kg in 1963 to 22 kg in 1972 and subsequently rose to 99 kg in 1978 or about one-half the 1963 value (Fig. 6). Winter flounder, longhorn sculpin, and winter skate appear to have remained fairly constant in abundance over the spring time period, while Atlantic cod, windowpane flounder, and little skate displayed an increasing trend in biomass (Fig. 9A). Yellowtail flounder and haddock showed declining mean catches over this interval. The fall time series, since it is longer, clarifies some of the observed spring trends. Cod and winter flounder CPUE remained relatively stable over the fall period, while windowpane flounder, winter skate, and little skate appear to have increased from 1972 onward (Fig.

FIGURE 6.—Mean catch per tow (kg) from NEFC Georges Bank bottom trawl surveys for autumn 1963-78 for the five assemblages. Dashed line indicates a 3-yr moving mean of the plotted data points.

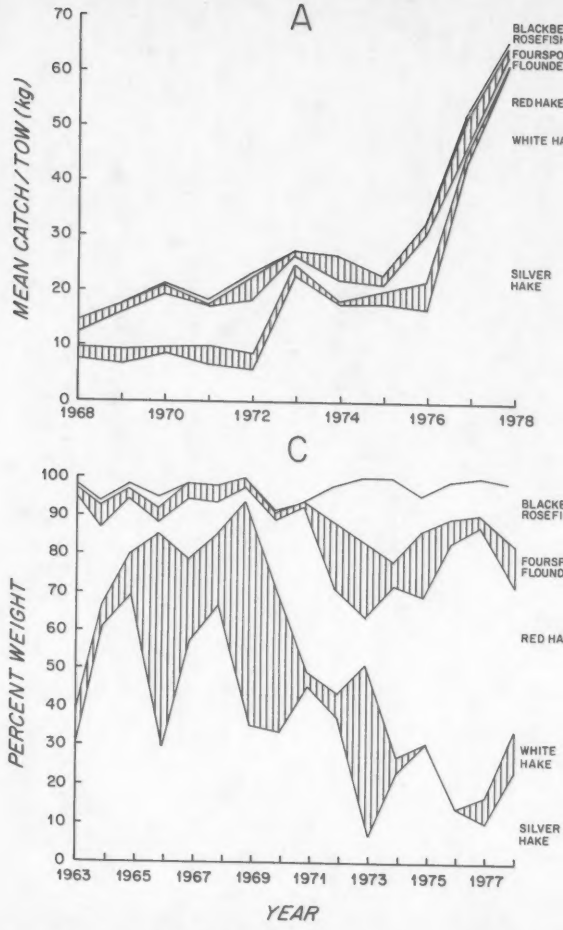
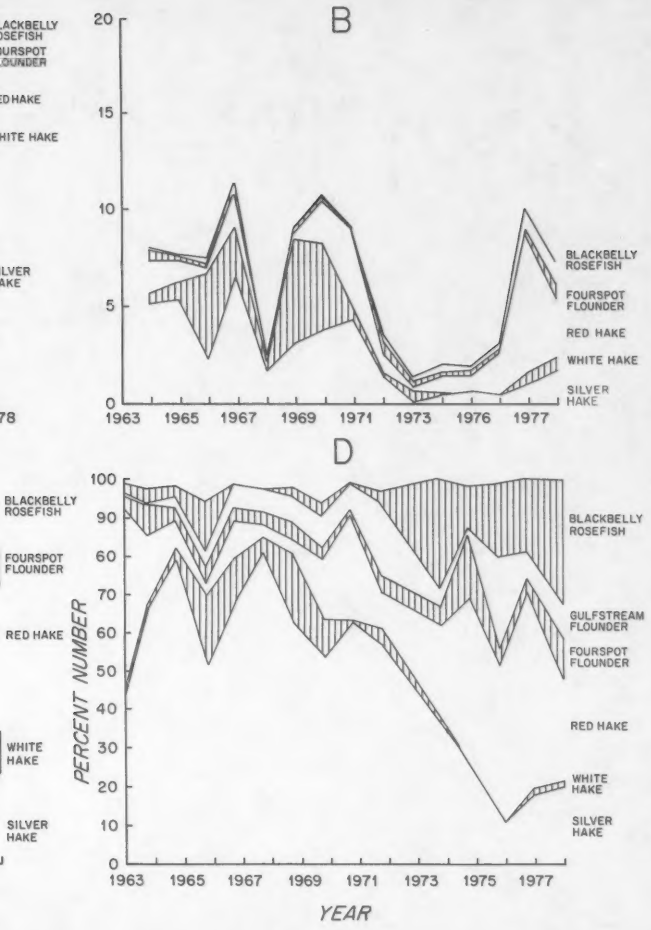


FIGURE 8.—Responses of species from the Slope and Canyon assemblage demersal fish community over the period 1963-78. Panels A and B express cumulative absolute abundance, mean catch/tow (kg) for spring 1968-78 and autumn 1963-78,



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respectively. Panels C and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

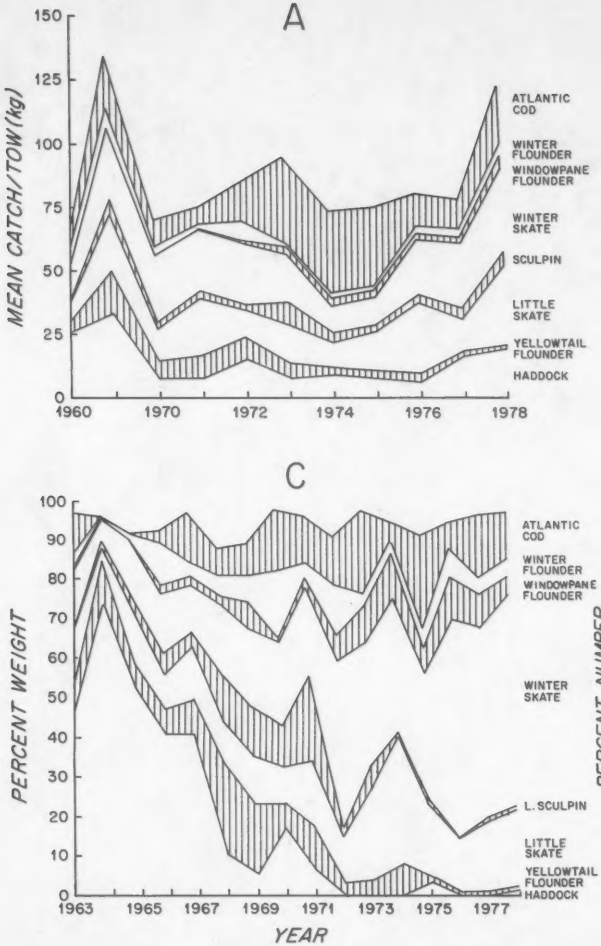
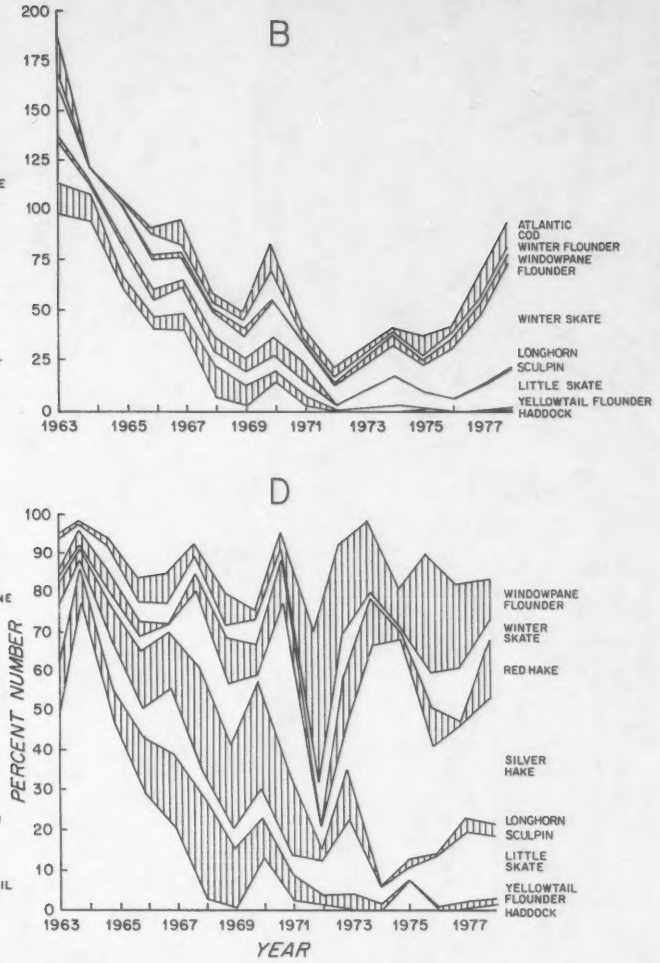


FIGURE 9.—Responses of species from the Shallow assemblage demersal fish communi
ty over the period 1963-78. Panels A and B express cumulative absolute abundance
mean catch/tow (kg) for spring 1968-78 and autumn 1963-78, respectively. Panels C



and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

9B). Haddock CPUE, on the other hand, declined dramatically from 97.3 kg in 1963 to 0 in 1972, remaining at very low levels of abundance in the later years. Yellowtail flounder fluctuated from 15 kg in 1963 to a low of 6 kg in 1966, increased from 1966 to 1969, and declined through 1978 (Fig. 8B).

An examination of trends in cumulative percent by weight and number trajectories for the Shallow assemblage highlighted some interesting points. Atlantic cod comprised a fairly constant proportion of the species biomass for all the years except 1964 and 1965. Longhorn sculpin, yellowtail flounder, and to a lesser extent winter flounder, made up an increasing part of the biomass of this assemblage during 1966-71 and then all declined in importance (Fig. 9C). Haddock, as previously noted, experienced a pronounced decline in abundance from the early 1960's and was only present at very low levels from 1972 to 1978. Winter skates, little skate, and windowpane flounder accounted for an increasing percent of the biomass in this assemblage from the early 1970's onward (Fig. 9C).

When cumulative percent by number was investigated, silver hake and red hake became important (Fig. 9D). Silver hake was the numerical dominant through most of the mid- and late 1970's. This trend was due entirely to increased numbers of juvenile silver hake that represented a small amount of biomass. This same phenomenon applies to red hake, which enjoyed several periods of increased abundance as a proportion of the total numerical density from 1963 to 1978. Winter skate numbers remained relatively unchanging from 1963 to 1976 and then rose slightly in the late 1970's. Trends for windowpane flounder, longhorn sculpin, little skate, yellowtail flounder, and haddock follow the cumulative absolute and percent weight data (Fig. 9B, C, D).

The other Georges Bank assemblages were investigated using the same techniques, but on a much less intense scale. Total mean catch/tow for the Intermediate, Gulf of Maine Deep, and Northeast Peak assemblages is displayed in Figure 6 for the fall surveys 1963-78. The trends in total CPUE follow the same basic patterns for all three groups, a high initial period followed by a decline and subsequent recovery in the mid- to late 1970's.

General decreases in the catch of throny skates, haddock, and cod were responsible for the downward trend in CPUE for the Northeast Peak assemblage, but the recovery that occurred in the late 1970's was due primarily to increased haddock biomass (Figs. 6, 10). The Northeast Peak assemblage is fairly simple in species composition, and although some fluctuations in cumulative percent by weight occurred, the same four species remained dominant over the period (Fig. 10.)

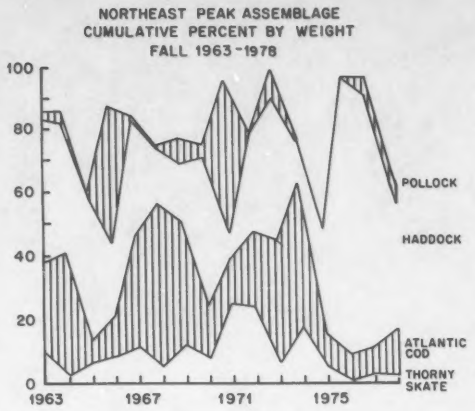


FIGURE 10.—Reponses of species from the Northeast Peak assemblage demersal fish community expressed as cumulative percent by weight for autumn 1963-78.

Time sequence cluster analyses were useful as further indicators of temporal trends in these groups. Species biomass for the Slope and Canyon assemblage did not appear to follow any clear long-term trend (Fig. 11). Enough fluctuation in CPUE occurred to mask any trend, and no clear pattern was established. This same analysis on the Shallow assemblage showed three distinct temporal clusters, composed of consecutive years (Fig. 11). Using this perspective and Figure 9, there appears to have been three periods of significant change in relative abundance during the fall time series; an initial period dominated by haddock, intermediate period with high yellowtail, longhorn sculpin, and winter flounder catches, and finally a group with little skate, winter skate, and windowpane flounder as the dominant species.

GRADIENT ANALYSIS

Gradient analyses of two selected Georges Bank data sets did not prove to be as useful as was hoped, but some information and insight were gained and the dimensionality of the large multivariate data sets involved was much reduced. The data set used in the fall 1976 canonical correlation analysis accounted for about 26% of the variation in species distribution for 32 selected species of interest. The variables included in the analysis were latitude, longitude, depth, bottom temperature, bottom salinity, and bottom oxy-

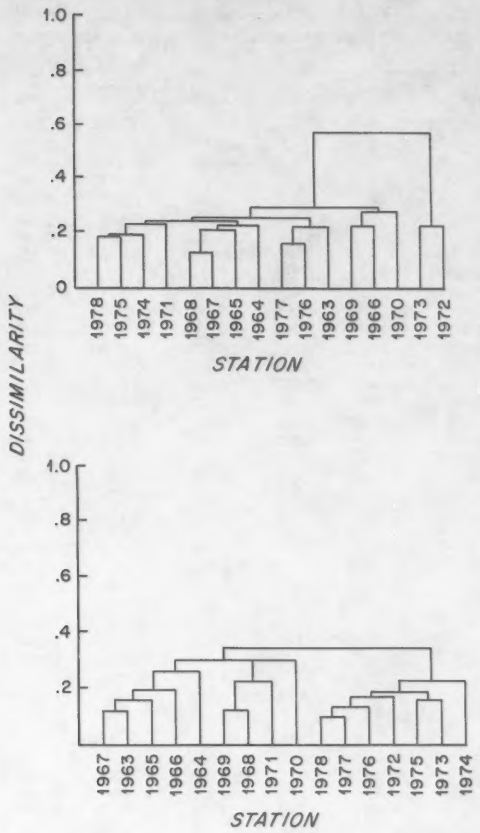


FIGURE 11.–Time sequence cluster analyses for autumn 1963-78 for the Slope and Canyon (top panel) and Shallow (bottom panel) assemblages on Georges Bank.

gen. The first three canonical axes accounted for 73.9% of this total, a cumulative redundancy of 19.0% (Table 3). The first canonical variable (CV) reflects the importance of depth and to a lesser degree bottom salinity, in determining the distribution of these species. Although none of the correlation loadings for CV1 are particularly high, the gadoids, as a group, show a positive trend. Many of the shallow-water species, such as little skate, winter skate, and most of the flounders, showed negative correlations with this canonical variable. The other two CV's reflect the location variables of latitude and longitude as well as bottom oxygen and salinity.

Since the gadoids and flounders appeared to show a group response to these distribution variables, we decided to use them in another analysis, excluding the other species (Table 3, Fall 1976 II). This data set explained 28.3% of the total variation in distribution for a selected set of 14 species (Table 3). The first canonical variable had a high correlation with latitude (r = 0.904) and the gadoids, as a group, were highly positively correlated with this CV (Table 3). It appears that although Georges Bank spans only about two degrees in total north-south latitudinal variation, this variable is useful for defining centers of gadoid biomass.

The third analysis did not reveal any new trends, accounting for 32.6% of the variation in species distribution. In general, then, although significant orthogonal canonical axes were defined in each of three data sets, the amount of variation that was actually explained was relatively small. There appear to have been trends in the distribution of some gadoid and flounder species, but the strength of these relationships was hardly firm. Most of the variation in species distribution was related to latitudinal, salinity, and depth differences.

DISCUSSION

Questions of community resilience (Pimm 1984) are meaningful because resource managers are faced with the dilemma of making decisions that may alter future community structure. Fishery managers, in particular, are unable to deal with the long-term consequences of their management decisions because they lack specific knowledge of ecosystem reponses. This idea may apply particularly to areas such as Georges Bank, where landings of each species are part of a multispecies otter trawl fishery. In this case the application of single species management to assemblages of fishes may result in simplification of the community such that less productive fish populations or those more vulnerable to fishing are reduced dramatically (Tyler et al. 1982). If this occurs, important trophic linkages may be precluded, economic viability may suffer, and management options may be removed indefinitely. At the present time the argument of these central issues is proceeding slowly in the literature and few, if any, management agencies are considering these types of questions in their decisions. We need, therefore, to begin to investigate the long-term temporal scale of communities so that ecologists and managers can begin to function in terms of ecological time instead of just a framework for short-term reaction.

Declines in total finfish abundance on the continental shelf of the northeastern United States reached unprecedented levels over the period 1965-74 (Brown et al. 1976). Not only had biomass declined,

TABLE 3.—Canonical variable (CV) loadings for fall 1976 and spring 1978 gradient analyses, with canonical correlation coefficients (Rc), amount of variation explained by each canonical axis (% variation), and total variation in species distribution explained by the environmental data.

	Fall 1976 I			Fall 1976 II			Spring 1978 I		
	CV1	CV2	CV3	CV1	CV2	CV3	CV1	CV2	CV3
Spiny dogfish	−0.509	0.149	0.232				−0.089	0.105	0.111
Winter skate	−0.263	0.342	−0.244				−0.176	−0.377	0.058
Little skate	−0.428	0.113	−0.163				−0.015	−0.437	0.142
Smooth skate	0.552	−0.117	−0.144				0.333	0.210	−0.204
Thorny skate	0.387	0.017	0.063				0.534	0.416	0.188
Sea herring	0.003	0.081	0.058				0.084	−0.147	0.068
Alewife	−0.023	0.097	0.161				0.433	0.086	0.104
Offshore hake	0.456	−0.408	−0.100	−0.147	0.613	0.284			
Silver hake	0.285	0.203	0.536	0.607	0.332	0.027	−0.237	0.637	−0.328
Atlantic cod	0.059	0.544	0.195	0.600	−0.263	0.048	0.262	−0.534	0.177
Haddock	0.370	0.525	0.131	0.647	−0.069	−0.235	0.383	−0.300	0.072
Pollock	0.337	0.158	0.199	0.439	0.274	0.167	0.425	0.209	0.015
White hake	0.564	−0.022	0.341	0.447	0.614	0.083	−0.030	0.527	0.055
Red hake	−0.109	−0.109	0.034	−0.220	−0.043	−0.460	0.303	0.616	0.057
American dab	0.281	0.048	0.362	0.395	0.365	0.141	0.409	−0.035	−0.026
Summer flounder	−0.245	−0.124	−0.102	−0.246	−0.111	0.126	−0.427	0.309	0.303
Fourspot flounder	−0.235	−0.265	0.210	−0.326	0.051	−0.588	−0.417	0.418	0.366
Yellowtail flounder	−0.158	0.324	−0.083	0.115	−0.419	−0.095	0.080	−0.442	0.144
Winter flounder	−0.145	0.364	0.078	0.295	−0.324	0.114	0.109	−0.301	0.040
Witch flounder	0.179	−0.267	0.140	−0.107	0.407	−0.187	0.368	0.138	−0.225
Windowpane	−0.326	0.165	−0.351	−0.087	−0.439	0.504	−0.527	0.041	0.251
Butterfish	−0.279	−0.415	0.405						
Blackbelly rosefish	0.359	−0.544	0.050				−0.295	0.529	−0.199
Longhorn sculpin	−0.078	0.432	−0.136				0.101	0.478	0.068
Sea raven	−0.034	0.432	−0.092				−0.500	0.034	0.194
Cunner	−0.082	0.198	0.023						
American sand lance	−0.134	0.043	−0.079				0.130	−0.125	0.224
Atlantic wolffish	0.011	0.240	0.106				0.233	0.073	0.358
Ocean pout	−0.043	0.265	0.122				−0.133	−0.316	0.034
American goosefish	0.145	−0.073	0.184				−0.261	0.414	−0.039
Short-finned squid	0.249	0.284	0.303				−0.275	0.169	0.072
Long-finned squid	−0.471	−0.239	−0.379				−0.256	0.399	−0.077
Variables									
Latitude	0.306	0.922	0.074	0.904	−0.333	0.066	0.878	0.012	−0.131
Longitude	−0.458	−0.164	0.597	−0.004	0.064	0.118	0.240	−0.032	0.474
Depth	0.885	−0.432	0.049	0.030	0.849	−0.071	−0.107	0.792	−0.448
Bottom temp.	−0.179	−0.696	−0.233	−0.590	0.258	0.366	−0.252	0.720	−0.465
Bottom salinity	0.463	−0.547	0.422	−0.107	0.753	−0.586	−0.374	0.909	−0.133
Bottom oxygen	−0.316	0.450	−0.581	0.041	−0.613	0.407	0.199	−0.908	0.144
RC	0.975	0.961	0.874	0.871	0.841	0.750	0.979	0.968	0.943
% variation	8.2	7.2	3.6	11.1	9.1	4.3	9.2	11.8	2.8
Significance	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Total variation		25.7			28.3			32.6	

but total effort on Georges Bank increased several times (Fig. 7). The assemblage trends examined in this paper can be linked to these high levels of effort.

During this time period, seasonal bottom trawl surveys monitored trends in finfish abundance over the area from the Gulf of Maine to Cape Hatteras. This survey proved invaluable to fish stock assessment work because changes in the relative abundance of most of the commercial species were followed closely and were highly correlated with commercial catch, effort, and other indices (Clark 1979). Other species of ecological, perhaps not commercial importance, were also routinely and closely monitored over this time. The spring and fall bottom trawl survey provided an excellent means for assessing community or assemblage responses over this time period.

Cluster analysis, with the Bray-Curtis dissimilarity index and group average fusion method, proved helpful for defining demersal fish assemblages on Georges Bank. Recent studies confirm the value and applicability of the Bray-Curtis index (Bloom 1981). This method provided a means for collapsing the multidimensional nature of the spring and fall Georges Bank survey cruises into smaller, more easily interpreted, units. It was then possible to investigate not only long-term temporal and spatial persistence questions, but also intraspecific responses within the particular assemblage of interest.

Not only did seasonal Georges Bank assemblages maintain their temporal integrity over the periods 1963-78 in the fall and 1968-78 in the spring, but they also appear to have retained their spatial configuration for the most part as well. The results of this study indicate that although changes in species composition and relative abundance occurred in varying degrees in all the assemblages, they remained continuous in time and space.

Although many of the species on Georges Bank are found in several assemblages, it appears that each of the five groups has enough large-scale variation in biomass, species composition, and relative abundance to make each of the assemblages unique. Also at least one or two dominant Georges Bank species occupy each assemblage, for example, the bulk of the haddock stock occurs in the Northeast Peak group. Thus, even though some assemblages changed dramatically in terms of species richness and relative abundance, the spatial integrity of each complex was preserved over time.

The energy budget of Georges Bank can serve as a plausible explanation for the particular species distributions we found. Georges Bank is a dynamic ecosystem driven by a complex and unique nutrient advection system. Its shallow topography and geographic location, with constant mixing of the water column and lack of stratification, does not lead to the usual nutrient limitation of primary productivity (Sutcliffe et al. 1976; Cohen et al. 1982). Instead of the usual spring and fall pulse in primary production, the region is characterized by high productivity from April to November. Yearly primary production levels are as high as 450 gC/m^2 per yr in the shallow (< 100 m) zone of Georges Bank (Cohen et al. 1982). This shallow mixed zone encompasses the same area as the Shallow and Intermediate assemblages delineated in our cluster analysis results. The area is dominated by fish that feed on invertebrates. Primary prey items for these species include euphausiids, copepods, mysids, amphipods, and other benthic invertebrates. This part of the ecosystem is fairly closely tied to primary production, and its component species may compete for food resources during their early life history (Pitt 1970; Bowman 1981; Overholtz 1982). Predation, too, may be an important biological mechanism for determing trends in this assemblage (Overholtz 1982). The other assemblages that we have described in this analysis occur along the fringes of Georges Bank at the shelf-slope interface. These shelf break groups contain the major adult demersal fish stocks found in the area with the exception of yellowtail flounder. These peripheral assemblages are dominated by large predators that are generally piscivorous, with little, if any, dietary overlap (Langton and Bowman 1981).

The gradient analyses suggest that about 25% of the total variation in species biomass distribution can be explained with the variables used in the study. This result was surprising at first, since we felt that the variables we used would explain much more of the variation than this. However, considering the fact that other important biological factors, such as predation, fishing, competition, and food preferences were not included in the analysis, it is probably a realistic percentage. Perhaps an analysis that included the whole east coast would account for much more variation because a wider range of conditions would exist.

Other studies that have successfully explained species distributions usually occur in habitats with very strong physical or chemical gradients, such as mountain forests or estuaries (Whitaker 1967; McIntire 1973). Either the actual gradients were not strong enough to explain more than a small percentage of the species distribution or those other factors were more important.

The questions of resilience and stability of demersal fish assemblages that were defined and investigated in this study have implications for the management of Georges Bank. This study provides a useful conceptual framework for managing many of the demersal fish stocks in this area. Not only were stable zones with specific resident fishes delineated, but they were present over the long-term record. Species components of fall assemblages are indicators of general distributions that represent the location of major fish stocks during the productive portion of the year. Long-term responses observed in the Georges Bank community indicate the propensity for adjustment or resilience (Holling 1973) that a particular assemblage might have. Assemblages on the periphery of Georges Bank might be less susceptible to changes in species composition and relative abundance because their component species are less trophically linked. The Shallow assemblage, on the other hand, appears to be particularly vulnerable to fishing and perhaps interspecific interactions. This type of knowledge will be helpful for understanding changes in fish abundance and community structure and for effectively managing fishery systems in the future.

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LITERATURE CITED

AZAROVITZ, T. R.
1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. Can. Spec. Publ. Fish. Aquat. Sci. 58:62-67.

BLOOM, S. A.
1981. Similarity indices in community studies: potential pitfalls. Mar. Ecol. Prog. Ser. 5:125-128.

BOESCH, D. F., AND R. C. SWARTZ.
1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environ. Prot. Agency Ecol. Res. Ser. EPA-600 3-77-033, 115 p.

BOWMAN, R. E.
1981. Food of 10 species of northwest Atlantic juvenile groundfish. Fish. Bull., U.S. 79:200-206.

BROWN, B. E., J. A. BRENNAN, M. D. GROSSLEIN, E. G. HEYERDAHL, AND R. C. HENNEMUTH.
1976. The effect of fishing on the marine finfish biomass in the Northwest Atlantic from the Gulf of Maine to Cape Hatteras. Int. Comm. Northwest Atl. Fish. Res. Bull. 12:49-68.

CLARK, S. H.
1979. Application of bottom trawl survey data to fish stock assessment. Fisheries (Bethesda) 4(3):9-15.

CLIFFORD, H. T., AND W. STEPHENSON.
1975. An introduction to numerical classification. Acad. Press, N.Y., 229 p.

COHEN, E. B., M. D. GROSSLEIN, M. P. SISSENWINE, AND F. STEIMLE.
1982. Energy budget of Georges Bank. *In* M. C. Mercer (editor), Multispecies approaches to fishery management advice, p. 95-107. Can. Spec. Publ. Fish. Aquat. Sci. No. 59, 169 p.

DEVRIES, T. J., AND W. G. PEARCY.
1982. Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record. Deep-Sea Res. 29: 87-109.

GABRIEL, W. L., AND A. V. TYLER.
1980. Preliminary analysis of Pacific Coast demersal fish assemblages. Mar. Fish. Rev. 42(3-4):83-88.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Comm. Fish. Rev. 31(8-9):22-30.

HOFF, J. G., AND R. M. IBARA.
1977. Factors affecting the seasonal abundance, composition, and diversity of fishes in a southeastern New England estuary. Estuarine Coastal Mar. Sci. 5:665-678.

HOLLING, C. S.
1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4:1-23.

INGLESIAS, J.
1981. Spatial and temporal changes in the demersal fish community of the Ria de Arosa (NW Spain). Mar. Biol. (Berl.) 65:199-208.

KENISTON, J. A.
1978. Program cluster: an aid to numerical classification using the CDC cyber computer. Oreg. State Univ. Sea Grant, Pleuronectid Proj. Tech. Rep. No. 2, 32 p. OSU Mar. Sci. Ctr., Newport, OR.

LANGTON, R. H., AND R. E. BOWMAN.
1981. Food of eight Northwest Atlantic pleuronectiform fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS, SSRF-749, 16 p.

MCINTIRE, C. D.
1973. The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estuarine Coastal Mar. Sci. 6:447-457.

OVERHOLTZ, W. J.
1982. Long-term temporal perspectives for the demersal fish assemblages of Georges Bank with implications for management and modeling. PhD. Thesis, Oregon State University, Corvallis, 259 p.

OVIATT, C. A., AND S. W. NIXON.
1973. The demersal fish of Narrangansett Bay: An analysis of community structure, distribution, and abundance. Estuarine Coastal Mar. Sci. 1:361-378.

PIMENTEL, R. A.
1979. Morphometrics: the multivariate analysis of biological data. Kendal/Hunt Publ. Co., Dubuque, Iowa.

PIMM, S. L.
1984. The complexity and stability of ecosystems. Nature (Lond.), 307:321-326.

PITT, T. K.
1970. Distribution, abundance, and spawning of yellowtail flounder, *Limanda ferrunginea*, in the Newfoundland area of the northwest Atlantic. J. Fish. Res. Board Can. 27:2261-2271.

RICHARDS, J., D. W. ARMSTRONG, J. R. G. HISLOP, A. S. JERMYN, AND M. D. NICHOLSON.
1978. Trends in Scottish research vessel catches of various fish species in the North Sea, 1922-1971. *In* G. Hempel (editor), North Sea fish stocks - recent changes and their causes, p. 211-224. Rapp. P.-V. Réun. 172, 449 p.

SMITH, S. H.
1972. Factors in ecological succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29:717-730.

SOUTAR, A., AND J. D. ISAACS.
1969. History of fish populations inferred from fish scales in anaerobic sediments off California. Calif. Coop. Oceanic Fish. Invest. Rep. 134:63-70.

STEPHENSON, W., AND M. C. L. DREDGE.
1976. Numerical analysis of fish catches from Serpentine Creek. Proc. R. Soc. Queensl. 87:33-43.

SUTCLIFFE, W. H., JR., R. H. LOUCKS, AND K. F. DRINKWATER.
1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33:98-115.

TYLER, A. V.
1971. Periodic and resident components in communities of Atlantic fishes. J. Fish. Res. Board Can. 28:935-946.

TYLER, A. V., W. L. GABRIEL, AND W. J. OVERHOLTZ.
1982. Adaptive management based on structure of fish assemblages of northern continental shelves. *In* M. C. Mercer (editor), Multispecies approaches to fishery management advice, p. 149-156. Can. Spec. Publ. Fish. Aquat. Sci. No. 59, 169 p.

WHITTAKER, R. H.
1967. Gradient analysis of vegetation. Biol. Rev. (Camb.) 42:207-264.

OBSERVER EFFECT ON INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA FISHERY

BRUCE E. WAHLEN[1] AND TIM D. SMITH[2]

ABSTRACT

Scientific observers placed aboard a sample of purse seine vessels collect data that are used to estimate the total number of dolphins killed incidentally in the eastern tropical Pacific tuna fishery. If the presence of these observers, who are not crew members, affects incidental kill levels, then the kill estimates will be biased. To test for the existence of such an observer effect, we compared dolphin kill data that had been recorded by observers who differed in levels of obtrusiveness according to their purposes for data collection. Some observers were placed on board primarily to collect data for estimating the total number of dolphins killed annually. Other observers collected data both for that purpose and for monitoring compliance with dolphin-release regulations. Our results confirm that the presence of an observer does affect dolphin kill. The primary effect is an increase in the proportion of sets with no dolphins killed, and a decrease in the proportion of sets with one to nine dolphins killed. While the magnitude of the effect of observers cannot be estimated from our data, estimates of total dolphin mortality based on data collected by the scientific observers are biased downward.

Schools of dolphins of several species, primarily *Stenella attenuata* and *S. longirostris*, have been used since the late 1950s by purse seine fishermen in the eastern tropical Pacific Ocean (ETP) to locate and catch yellowfin tuna, *Thunnus albacares*. Perrin (1969) described the process of deploying, or setting, the net around the tuna and dolphins, and then releasing the dolphins while retaining the tuna. Significant numbers of dolphins have been killed incidentally in this fishery by becoming entangled in the purse seines (Smith 1983).

The National Marine Fisheries Service (NMFS) and the Inter-American Tropical Tuna Commission (IATTC) place scientific observers who are not crew members aboard a sample of tuna purse seine vessels to collect data related to dolphin kill. Both the NMFS and IATTC have used the data collected by these scientific observers to estimate the total number of dolphins killed annually by the entire tuna purse seine fleet (Lo et al. 1982; Hammond and Tsai 1983).

Additionally, the NMFS uses these data to monitor dolphin kills relative to annual kill limits established for the U.S. registered fleet (Lo et al. 1982). Periodic estimates of the cumulative numbers of dolphins killed are compared with the annual limit. If the limit is exceeded, U.S. vessels must stop fishing on the affected populations for the remainder of the year.

Data collected by the NMFS observers have also been used to monitor compliance of vessel operators with dolphin-release regulations, including the release of all live dolphins from the net (Federal Register 1977, 1980). Until recently, data collected by an NMFS observer could be used as evidence to prosecute vessel operators for violations of these regulations.

Observer effects have been defined in a general context as measurement procedures which influence and thereby change the behavior of the subject (Johnson and Bolstad 1973, p. 38). Researchers have encountered such effects in a variety of empirical sciences, including psychology (Johnson and Bolstad 1973), social science (Webb et al. 1966, p. 18), and biology (Ricker 1975, p. 87).

We defined an observer effect on the number of dolphins killed as a differential in levels of dolphin kill between trips made with and without a scientific observer. The existence of such a differential would introduce a bias into estimates of the total number of dolphins killed (Smith 1983; Powers[3]). Large numbers of sets involving dolphins (dolphin sets) are made each year (Punsly 1983), so even a moderate observer effect could result in a substan-

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[3]Powers, J. E. 1979. A discussion of incidental mortality by unobserved United States purse seiners. Unpubl. manuscr., 7 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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tial bias in the estimates of annual dolphin kill.

Directly testing for the existence of an observer effect on dolphin kills would require comparison of covert observations with observations by NMFS and IATTC observers. Based on the large difference between the kill rate observed covertly by one crew member and the kill rates recorded by NMFS observers during other fishing trips made by the same operator and vessel, Smith (1983) speculated that a large observer effect existed. We investigated the significance of the difference in kill rates reported by Smith (1983) by grouping NMFS-observed trips into sequences of trips with common operator and vessel. A few of these sequences of NMFS-observed trips revealed between-trip kill rate differences as large or larger than in the sequence that included the covert observations.

The existence of an observer effect can be indirectly tested without relying on data from covert observers. Johnson and Bolstad (1973) established the existence of an observer effect by comparing measurements made by observers with various levels of obtrusiveness to the human subjects whose responses were being measured. They concluded that the differences in the responses measured by observers with different levels of obtrusiveness implied that the observer's presence had affected the subjects' behavior. They noted, however, that the magnitude of an observer effect cannot be estimated using this approach.

Following this indirect approach, we tested for the existence of an observer effect on the numbers of dolphins killed by comparing dolphin kill data collected by scientific observers who differed in their purposes of data collection, and hence, in their levels of obtrusiveness.

DATA

The scientific observers were placed aboard a random sample of U.S. registered tuna purse seine vessels (Lo et al. 1982). Assignment of an NMFS or IATTC observer to vessels in the sample was also made randomly, subject to the constraint that any vessel sampled twice within a calendar year would be accompanied by an NMFS observer on at most one trip (Table 1).

Information collected for each NMFS- or IATTC-sampled fishing trip included departure date and data pertaining to each set (such as set type, date, and location), and for dolphin sets, the number of dolphins killed. Data available to the authors from NMFS-sampled trips included all of this information. However, data available from IATTC-sampled trips did not include departure date, and set dates were available only to the quarter of the year.

While the data items collected by both types of scientific observer have been similar over the years, for NMFS observers the purposes of the data collection changed after March 1981. The primary purposes of data collection, as explained to each vessel operator at a placement meeting held prior to departure, were as follows: 1) On NMFS-sampled trips begun from 1978 through March 1981, data were collected for estimating the annual kill of dolphins and for monitoring compliance with dolphin-release regulations; 2) on NMFS-sampled trips begun after March 1981 through the end of 1982, the data were still used for estimating dolphin kills but were no longer used to monitor compliance with dolphin-release regulations[4]; 3) on all IATTC-sampled trips, since the inception of that sampling program in 1979, data were collected for estimating total kill but were never collected for monitoring compliance with dolphin-release regulations.

As described above, the data collected by both NMFS and IATTC observers to estimate total dolphin kill can be used by the NMFS to halt fishing by U.S. vessels on specific dolphin populations for the remainder of the year. The data collected before March 1981 by the NMFS observers for monitoring compliance with dolphin-release regulations, however, can be used by the NMFS as evidence to prosecute operators who failed to comply. Thus, the operators are likely to be more conscious of the presence of an observer who is collecting data both for estimating dolphin kill and for monitoring com-

[4]The change in data collection purposes of NMFS observers after March 1981 was prompted by a court order forbidding the NMFS from using data collected by observers for monitoring compliance with dolphin-release regulations. No NMFS observers were placed on fishing trips begun from 1983 through part of 1984 because of a subsequent court order forbidding placement of NMFS observers without a search warrant.

TABLE 1.—Number of observed fishing trips which made at least one dolphin set from 1978 through 1982, by observer type and year. NMFS totals are subdivided according to departure date of trips (previous year, Jan.-Mar., Apr.-Dec.) and exclude trips in which fishing gear research was conducted.

Observer type	1978	1979	1980	1981	1982
NMFS					
Previous year	5	4	3	3	7
Jan.-Mar.	44	33	15	7	13
Apr.-Dec.	56	32	28	28	18
Total	105	69	46	38	38
IATTC	0	31	57	58	44
Total	105	100	103	96	82

pliance with dolphin-release regulations than an observer who is collecting data only for estimating dolphin kill. That this is the case is implied by the constraint in the sampling procedure that any vessel sampled twice within a calendar year may be accompanied by an NMFS observer on at most one trip.

METHODS

We tested for the existence of an observer effect on dolphin kills by comparing the number of killed dolphins recorded by more obtrusive observers with the number recorded by less obtrusive observers. We considered observers who collected data both for estimating dolphin kill and for monitoring compliance with dolphin-release regulations to be more obtrusive to vessel operators than observers who collected data only for estimating dolphin kill. Thus, we compared kills recorded by (1a) NMFS observers before and after March 1981, and (1b) NMFS and IATTC observers before March 1981. As a control, we compared the number of killed dolphins recorded by observers of equal obtrusiveness. That is, we compared kills recorded by (2a) IATTC observers before and after March 1981, and (2b) NMFS and IATTC observers after March 1981.

The frequency distributions of numbers of dolphins killed were extremely skewed, with very long right tails (Fig . 1). Normality assumptions were violated so strongly by these skewed distributions that ANOVA tests for differences in means, particularly one-sided tests, would be difficult to interpret (Glass et al. 1972). Therefore, we tested for differences in the percent of dolphin sets in which no dolphins were killed (zero-kill sets). This percent relates directly to the regulation requiring release of all live dolphins, and is a dominant feature of the dolphin kill distributions.

When comparing frequency distributions, we entertained the null hypothesis of equality of percent zero-kill sets. When comparing observers of different obtrusiveness levels, we tested this hypothesis against a one-sided alternative that distributions from more obtrusive observers had a higher percent

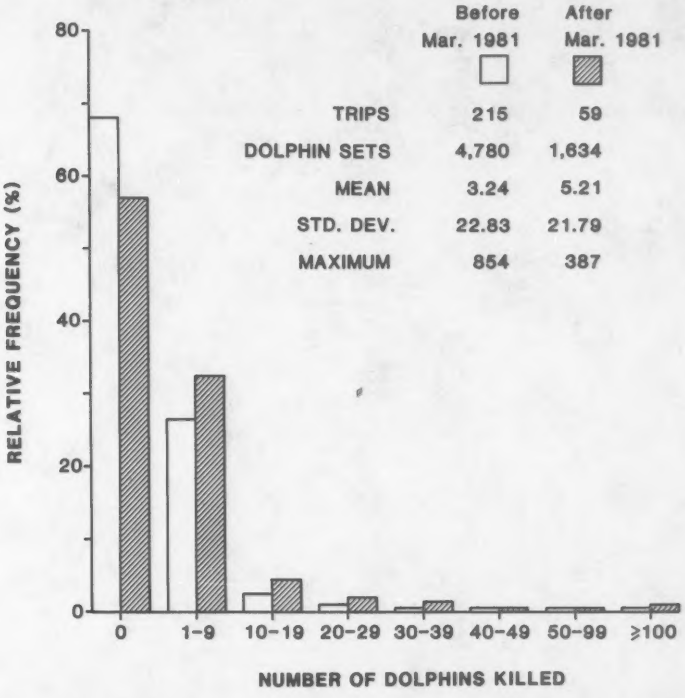

FIGURE 1.—Relative frequency distributions of number of dolphins killed incidentally during sets of NMFS-observed trips, 1978 through 1982, by trip departure date.

of zero-kill sets than distributions from less obtrusive observers. When comparing distributions from observers of equal obtrusiveness, we tested the null hypothesis against the two-sided alternate of inequality (Table 2). Results from all of our tests are reported at the 0.05 significance level.

TABLE 2.—Alternate hypotheses to the null hypothesis of equality of percent zero-kill sets for each of four comparisons, where Before and After refer to before or after March 1981. See text for details.

Comparison		Alternate hypothesis
1a.	NMFS before vs NMFS after	Before > After
2a.	IATTC before vs IATTC after	Before ≠ After
1b.	NMFS before vs IATTC before	NMFS > IATTC
2b.	NMFS after vs IATTC after	NMFS ≠ IATTC

For two-sided tests of differences in percents, we used the standard chi-square (χ^2) statistic with one degree of freedom (df). For one-sided tests, we used the square root of the chi-square statistic (Z), which is approximately normal (Snedecor and Cochran 1980, p. 126-127). In some instances, the expected cell frequencies were less than the traditionally accepted minimum of five. However, recent Monte Carlo results (Fienberg 1980, p. 172) suggest that the chi-squared distribution is an adequate approximation at the 0.05 significance level even when minimum expected values are as low as one.

While the sampling of vessels was nearly random, the actual sample obtained may not have been representative of factors affecting dolphin kills. It has been demonstrated that within the ETP, dolphin kills vary among three geographic areas[5] (Fig. 2) and by periods within the year (Lo et al. 1982). We divided the year into two periods: January-March and April-December. This division corresponds to the date of the change in data collection purposes of NMFS observers in 1981, and also tends to equalize sample size since vessels in this fishery are more active in the early part of the year.

We stratified the data by area and period of the year to account for biases due to possible nonrepresentativeness of the sample with respect to these two factors. When data on numbers of dolphins killed were available in all six area-period strata, we made overall two-sided tests for differences in per-

[5]K.T. Tsai, Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92093, pers. commun. December 1983.

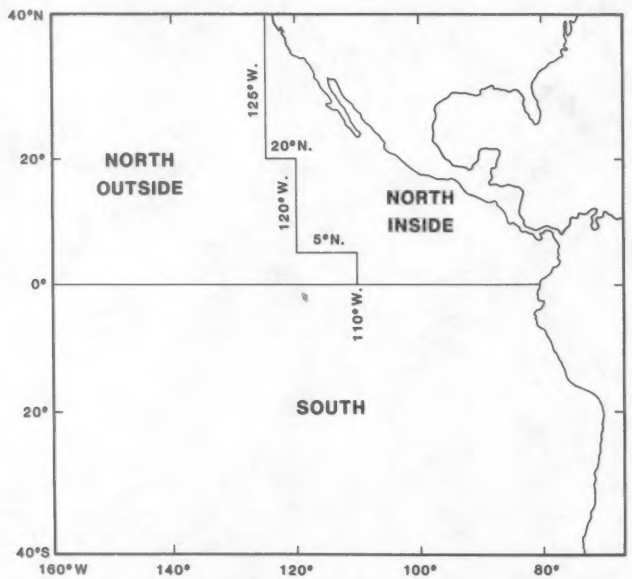

FIGURE 2.—The three areas of the eastern tropical Pacific used to stratify the data, bounded by lat. 40°N., long. 160°W., lat. 40°S., and the western coastline of the North and South American Continents.

cent zero-kill sets (conditional on period of the year and geographic area) by summing chi-square values and degrees of freedom from each stratum. When observations were not available in one of the strata, or when the alternative was one-sided, an overall test based on the chi-square statistic was not possible. In those cases, results of the tests within each stratum were considered separately.

RESULTS

The first two comparisons of frequency distributions test for differences in the percent of zero-kill sets in data collected by observers on trips begun before compared with trips begun after the change in NMFS observer data collection purposes in March 1981 (Comparisons 1a and 2a, Table 2). The last two comparisons test for differences in the percent of zero-kill sets in data collected by observers on trips begun during the same time period (Comparisons 1b and 2b, Table 2).

Before versus After

The percent of zero-kill sets for NMFS-observed trips was higher before March 1981 than after that date (Fig. 1), and within all area-period strata with complete data, the percent of zero-kill sets was larger before March 1981 (Table 3). The one-sided test of this difference (Comparison 1a, Table 2) was significant within four of the five area-period strata which had complete data, and was very nearly significant within the fifth (Table 3). Thus, the percent of zero-kill sets recorded by NMFS observers was significantly larger before March 1981.

The significant difference in percent of zero-kill sets for NMFS observers before compared with after March 1981 could be due to the change in data collection purposes of NMFS observers which occurred then. Alternatively, the difference could be due to a temporal decline begun before that date.

Allowing for period, the data prior to March 1981 do not show a pronounced trend for any of the three areas (Fig. 3). Although there appears to be a decline in the South for Period 2, this is unreliable as it depends entirely on the 1980 and 1981 data points representing a total of only 17 sets. Similarly, there seems to be a declining trend for the two northern areas. However, for the North Inside area the Period 1 points show no decline, and the possible decline of Period 2 points depends on the 1980 Period 2 point. A 95% confidence interval about this point (observed percent $\pm 2 \times$ standard error), however, is large relative to the difference between it and the Period 2 point of 1979. Further, any such declining trend in Period 2 points for the North Inside area is not reflected in the low 1978 point. A similar argument can be made for North Outside area data to reject the alternative explanation of the difference in percent zero-kill sets before and after March 1981 being the result of a temporal trend begun prior to March 1981.

That the differences in percent of zero-kill sets for NMFS-observed trips was not due to a temporal trend was also tested by comparing the percent of such sets for IATTC-observed trips before and after March 1981. The percent of zero-kill sets for IATTC-observed trips was higher before March 1981, but within the six area-period strata the differences were not consistent (Table 4). The two-sided test (Comparison 2a, Table 2) was significant within only one of the six area-period strata (Period 1, South), and the sample size within that stratum was very small (Table 4). The overall conditional test given area and period was not significant. Thus, IATTC-observed trips with dolphin sets from 1979 through 1982 did

TABLE 3.—Numbers of dolphin sets (*n*) made during NMFS-observed trips, 1978 through 1982. Sets are classified by trip departure date relative to March 1981 (before or after) and to period (1 = Jan.-Mar., 2 = Apr.-Dec.), by area of set (North Inside, North Outside, South), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (*e*), and the statistic *Z* are also tabulated. Values of $Z > 1.64$ are significant, as indicated by an asterisk.

		Period 1						Period 2						Total	
		North Inside		North Outside		South		North Inside		North Outside		South			
Kill		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
0	*n*	1,498	226	0	21	107	0	972	421	591	229	86	33	3,254	930
	%	72.9	62.1	—	52.5	61.1	0.0	69.4	62.7	60.4	55.7	50.6	23.1	68.1	56.9
	e	1,464.7	259.3	0	21	104.0	3.0	941.9	451.1	577.4	242.6	64.6	54.4	—	—
>0	*n*	558	138	0	19	68	5	429	250	387	182	84	110	1,526	704
	%	27.1	37.9	—	47.5	38.9	100.0	30.6	37.3	39.6	44.3	49.4	76.9	31.9	43.1
	e	591.3	104.7	0	19	71.0	2.0	459.1	219.9	400.6	168.4	105.4	88.6	—	—
Total	*n*	2,056	364	0	40	175	5	1,401	671	978	411	170	143	4,780	1,634
	Z	4.18*		—		2.75*		3.01*		1.63		4.99*		—[1]	

[1]Computation of overall test statistic not possible because of one-sided alternative, and because of lack of data in one stratum (Period 1, North Outside).

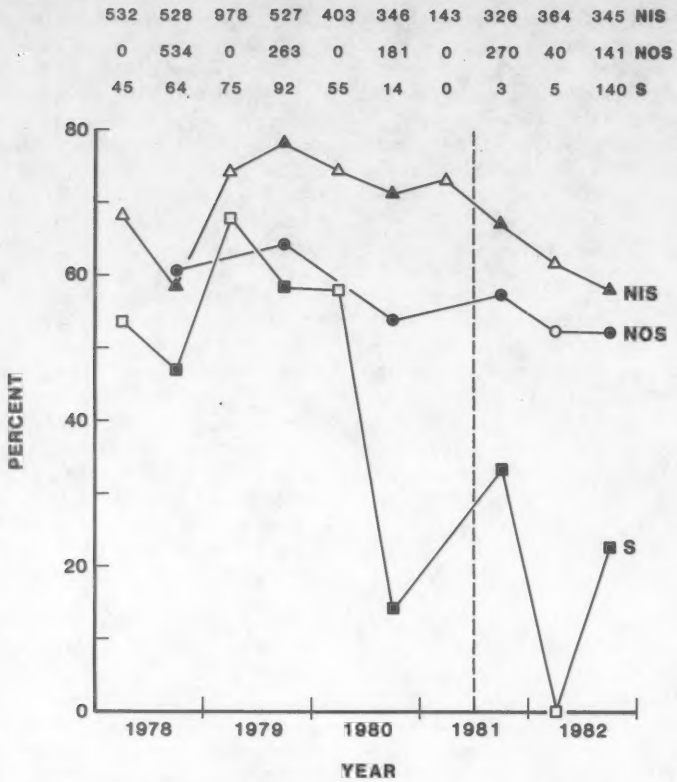

FIGURE 3.—Number of dolphin sets (upper portion) and percent of zero-kill dolphin sets (lower portion) for each of 3 areas (NIS = North Inside, NOS = North Outside, S = South) by period within year (open symbol = Jan.-Mar., closed symbol = Apr.-Dec.). Data are from NMFS-observed trips, 1978 through 1982. Vertical line separates data before and after March 1981.

TABLE 4.—Numbers of dolphin sets (*n*) made from 1979 through 1982, during IATTC-observed trips. Sets are classified by date of set relative to March 1981 (before or after) and to period (1 = Jan.-Mar., 2 = Apr.-Dec), by area of set (North Inside, North Outside, South), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (*e*), and the statistic χ^2 with degrees of freedom (df) are also tabulated. Values of $\chi^2 > 3.84$ (1 df) or 12.59 (6 df) are significant, as indicated by an asterisk.

		Period 1						Period 2							
		North Inside		North Outside		South		North Inside		North Outside		South		Total	
Kill		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
0	*n*	537	188	9	3	13	3	709	721	291	328	5	35	1,564	1,278
	%	67.1	71.2	26.5	14.3	38.2	12.0	70.0	70.1	58.7	55.6	33.3	24.1	65.4	61.6
	e	545.1	179.9	7.4	4.6	9.2	6.8	709.8	720.2	282.7	336.3	3.8	36.2	—	—
>0	*n*	263	76	25	18	21	22	304	307	205	262	10	110	828	795
	%	32.9	28.8	73.5	85.7	61.8	88.0	30.0	29.9	41.3	44.4	66.7	75.9	34.6	38.4
	e	254.9	84.1	26.6	16.4	24.8	18.2	303.2	307.8	213.3	253.7	11.2	108.8	—	—
Total	*n*	800	264	34	21	34	25	1,013	1,028	496	590	15	145	2,392	2,073
	χ^2	1.53		1.13		5.02*		0.01		1.04		0.61		9.34	
	df	1		1		1		1		1		1		6	

not differ significantly in their percent of zero-kill sets before or after March 1981.

Same Time Period

Before March 1981 the percent of zero-kill sets was higher for NMFS-observed trips than for IATTC-observed trips (Fig. 4), and within all area-period strata with complete data, the percent of zero-kill sets was larger for the NMFS observers (Table 5). The one-sided test (Comparison 1b, Table 2) was significant within four of the five area-period strata which had complete data (Table 5). Thus, for trips making dolphin sets from 1979 through March 1981, NMFS observers recorded a significantly higher percent of zero-kill sets than did IATTC observers.

According to our hypothesis, the difference in percent of zero-kill sets between NMFS- and IATTC-observed trips before March 1981 should have disappeared after March 1981 when the purposes for data collection of NMFS observers became nearly the same as for IATTC observers. After March 1981 the percent of zero-kill sets was higher for IATTC-observed trips than for NMFS-observed trips (Fig. 5), but within the six area-period strata the differences were not consistent (Table 6). The two-sided test (Comparison 2b, Table 2) was significant within only one of the six area-period strata (Period 1, North Inside), yet this one chi-square statistic was so large that the overall conditional test for all six strata was also significant (Table 6). It is difficult to interpret the overall result in this situation because of the extraordinary influence of one stratum. However, after March 1981 the percent of zero-kill sets on NMFS-observed trips was clearly not higher than on IATTC-observed trips.

While one would expect the mean number of dolphins killed to decrease when the percent of zero-kill sets increases, this is not necessarily so because of the sensitivity of the mean of a sample to the maximum value in the sample. For instance, in Figure 4 the NMFS maximum is nearly twice that of the IATTC, resulting in a larger NMFS mean despite the higher percent of zero-kill sets in the NMFS sample.

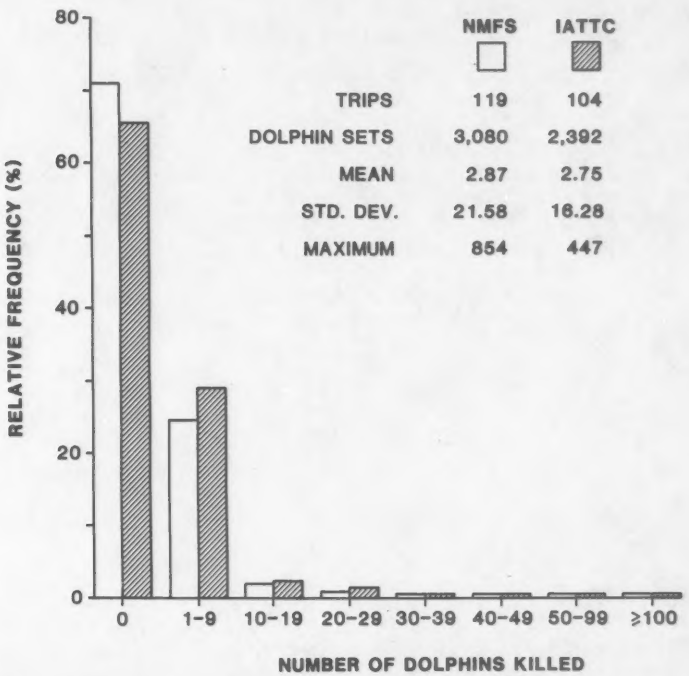

FIGURE 4.—Relative frequency distributions of number of dolphins killed incidentally during sets made from 1979 through March 1981, by observer type.

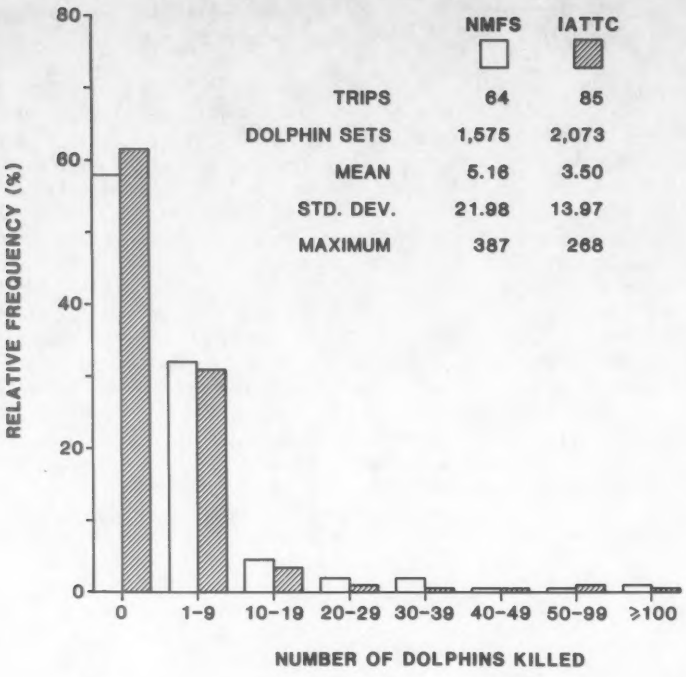

FIGURE 5.—Relative frequency distributions of number of dolphins killed incidentally during sets made after March 1981 through 1982, by observer type.

TABLE 5.—Numbers of dolphin sets (*n*) made from 1979 through March 1981. Sets are classified by observer type (NMFS, IATTC), by area of set (North Inside, North Outside, South), by date of set relative to period (1 = Jan.-Mar., 2 = Apr.-Dec.), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (*e*), and the statistic *Z* are also tabulated. Values of $Z > 1.64$ are significant, as indicated by an asterisk.

		Period 1						Period 2						Total	
		North Inside		North Outside		South		North Inside		North Outside		South			
Kill		NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC
0	*n*	820	537	0	9	96	13	942	709	267	291	62	5	2,187	1,564
	%	72.7	67.1	—	26.5	53.9	38.2	76.8	70.0	60.1	58.7	59.6	33.3	71.0	65.4
	e	793.9	563.1	0	9	91.5	17.5	904.0	747.0	263.6	294.4	58.6	8.4	—	—
>0	*n*	308	263	0	25	82	21	284	304	177	205	42	10	893	828
	%	27.3	32.9	—	73.5	46.1	61.8	23.2	30.0	39.9	41.3	40.4	66.7	29.0	34.6
	e	334.1	236.9	0	25	86.5	16.5	322.0	266.0	180.4	201.6	45.4	6.6	—	—
Total	*n*	1,128	800	0	34	178	34	1,226	1,013	444	496	104	15	3,080	2,392
	Z	2.64*		—		1.68*		3.66*		0.46		1.92*		—[1]	

[1]Computation of overall test statistic not possible because of one-sided alternative, and because of lack of data in one stratum (Period 1, North Outside).

DISCUSSION AND CONCLUSIONS

We established the existence of an observer effect on the number of dolphins killed incidentally in the ETP yellowfin tuna fishery by following two lines of argument. First, we demonstrated a decrease in the percent of sets with no dolphins killed on NMFS-observed trips after March 1981, when monitoring compliance with dolphin-release regulations was removed as a data collection purpose (Table 3). We further showed that this difference was not due to a temporal trend in fishing conditions by examin-

TABLE 6.—Numbers of dolphin sets (*n*) made from April 1981 through 1982. Sets are classified by observer type (NMFS, IATTC), by area of set (North Inside, North Outside, South), by date of set relative to period (1 = Jan.-Mar., 2 = Apr.-Dec.), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (*e*), and the statistic χ^2 with degrees of freedom (df) are also tabulated. Values of $\chi^2 > 3.84$ (1 df) or 12.59 (6 df) are significant, as indicated by an asterisk.

		Period 1						Period 2						Total	
		North Inside		North Outside		South		North Inside		North Outside		South			
Kill		NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC
0	*n*	193	188	1	3	1	3	455	721	249	328	13	35	912	1,278
	%	55.6	71.2	14.3	14.3	10.0	12.0	66.4	70.1	56.1	55.6	15.9	24.1	57.9	61.6
	e	216.4	164.6	1.0	3.0	1.1	2.9	470.3	705.7	247.8	329.2	17.3	30.7	—	—
>0	*n*	154	76	6	18	9	22	230	307	195	262	69	110	663	795
	%	44.4	28.8	85.7	85.7	90.0	88.0	33.6	29.9	43.9	44.4	84.1	75.9	42.1	38.4
	e	130.6	99.4	6.0	18.0	8.9	22.1	214.7	322.3	196.2	260.8	64.7	114.3	—	—
Total	*n*	347	264	7	21	10	25	685	1,028	444	590	82	145	1,575	2,073
	χ^2	15.53*		0.00		0.03		2.63		0.02		2.16		20.37*	
	df	1		1		1		1		1		1		6	

ing the data by period (Fig. 3) and by demonstrating the lack of a corresponding change in data collected by IATTC observers (Table 4).

Second, we demonstrated that before March 1981 the percent of sets with no dolphins killed was higher for NMFS observers collecting data both for estimating dolphin kill and for monitoring compliance with dolphin-release regulations than for IATTC observers collecting data only for estimating dolphin kill (Table 5). To validate this comparison we also demonstrated that the difference disappeared, or perhaps was reversed, following March 1981 when monitoring compliance with dolphin-release regulations was removed from the NMFS observers' responsibilities (Table 6). Following Johnson and Bolstad (1973), these differences in the data collected by observers differing in their purposes of data collection, and hence in their obtrusiveness, imply the existence of an observer effect.

In making these comparisons, we stratified the data to account for possible differences in fishing conditions in different geographic areas and throughout the year because both area and time of year are important determinants of dolphin mortality. Thus, the differences in the percent of zero-kill sets which we identified cannot be attributed to nonrepresentativeness of the data with respect to area and time of year.

We did not attempt to test for other differences in the frequency distributions of kills, such as changes in the percent of moderate or large kill sets. Sets with large numbers of dolphins killed are rare, and are generally associated with unusual circumstances, such as mechanical failures. The percent of sets with 1-9 dolphins killed appears to vary inversely with the percent of sets with zero dolphins killed (Figs. 1, 4, 5).

Powers et al.[6] showed that the use of some dolphin-release procedures significantly reduces dolphin mortality. Thus, more time and effort expended by the operator on release of dolphins could result in an increase in the frequency of sets with no dolphins killed, and a corresponding decrease in the frequency of sets with 1-9 dolphins killed. A greater tendency for vessel operators to take the additional time in the presence of an observer collecting data for monitoring compliance with dolphin-release regulations could account for the differences we have demonstrated.

The significantly different relative frequency of zero-kill sets recorded by NMFS observers after March 1981 (Table 6) was not expected under our hypothesis. As noted above, this difference was localized to one area-period stratum, and the other five strata were consistent with the null hypothesis of no difference. Either this difference is merely a sampling anomaly, or there are differences between observers in more recent years that we have not taken into account.

Gulland (1983, p. 111) described a method of testing for the existence of a tagging effect that is analogous to our indirect method of testing for an observer effect. He suggested comparing the proportions of tags returned from fish tagged under poor and good conditions. In both Gulland's and our methods, the absolute magnitude of the effects cannot be estimated. For instance, in Gulland's example improvement in the conditions under which tags are applied is unlikely to eliminate entirely the tagging effect. Similarly, the reduction in observer ob-

[6]Powers, J. E., N. C. H. Lo, and B. E. Wahlen. 1979. A statistical analysis on effectiveness of porpoise rescue procedures in reducing incidental mortality. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-7, 29 p.

trusiveness after March 1981 is unlikely to have eliminated entirely the observer effect because the data collected by scientific observers after 1981 were still used to monitor dolphin kills relative to annual kill limits. Observers collecting data that could not be used for monitoring kill limits would be even less obtrusive than the scientific observers, and covert observers would be, of course, completely unobtrusive.

Based on our analysis, we would expect that the frequency of zero-kill sets would be lower on unobserved vessels than on vessels with a scientific observer. This lower frequency of zero-kill sets, coupled with an increased frequency of sets with 1-9 dolphins killed, suggests that the average kill rate on unobserved vessels would be higher. Estimates of total kill, based on the average kill rates from the scientific observers, would therefore be underestimated.

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LITERATURE CITED

FEDERAL REGISTER.
1977. Department of Commerce, NOAA, Taking of marine mammals incidental to commercial fishing operations; final decision and final regulations. Fed. Regist. 42(247):64548-64560.

FEDERAL REGISTER.
1980. Department of Commerce, NOAA, Taking of marine mammals incidental to commercial fishing operations—permits, etc. Fed. Regist. 45(213):72178-72196.

FIENBERG, S. E.
1980. The analysis of cross-classified categorical data. 2d ed. MIT Press, Cambridge, MA, 198 p.

GLASS, G. V., P. D. PECKHAM, AND J. R. SANDERS.
1972. Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. Rev. Educ. Res. 42(3):237-288.

GULLAND, J. A.
1983. Fish stock assessment: a manual of basic methods. John Wiley and Sons, N.Y., 223 p.

HAMMOND, P. S., AND K.-T. TSAI.
1983. Dolphin mortality incidental to purse-seining for tunas in the eastern Pacific Ocean, 1979-81. Rep. Int. Whaling Comm. 33:589-597.

JOHNSON, S. M., AND O. D. BOLSTAD.
1973. Methodological issues in naturalistic observation: some problems and solutions for field research. *In* L. A. Hamerlynck, L. C. Handy, and E. J. Mash (editors), Behavior change: methodology, concepts, and practice, p. 7-67. Research Press, Champaign, IL.

LO, N. C. H., J. E. POWERS, AND B. E. WAHLEN.
1982. Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse seine fishery. Fish. Bull., U.S. 80:396-401.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6): 42-45.

PUNSLY, R. G.
1983. Estimation of the number of purse-seiner sets on tuna associated with dolphins in the eastern Pacific Ocean during 1959-1980. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull. 18:229-299.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull., U.S. 81:1-13.

SNEDECOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. 7th ed. Iowa State University Press, Ames, IA, 507 p.

WEBB, E. J., D. T. CAMPBELL, R. D. SCHWARTZ, AND L. SECHREST.
1966. Unobtrusive measures: a survey of non-reactive research in the social sciences. Rand McNally, Chic., 225 p.

FOOD HABITS OF JUVENILE ROCKFISHES (*SEBASTES*) IN A CENTRAL CALIFORNIA KELP FOREST

MICHAEL M. SINGER[1]

ABSTRACT

The diets and feeding morphology of juveniles of seven rockfish species (Scorpaenidae: *Sebastes*) were investigated in a kelp forest at Stillwater Cove, Carmel Bay, CA. The seven species could be divided into two groups, those which fed primarily on open water prey in the water column and those which fed on substrate-associated prey. Substrate-associated prey were generally larger than open water prey and were eaten by predators with relatively larger heads and mouths and shorter gill rakers. Comparison of juvenile diets and foraging patterns with those of adults showed that both foraged in similar manners and in the same general habitats. The absence of aggressive interactions within or among species and high intraspecific variability of foraging patterns suggests that little interference or exploitative competition was present.

Most of the literature on rockfishes deals mainly with aspects of either adult or larval biology (DeLacey et al. 1964; Phillips 1964; Miller and Geibel 1973; Westrheim 1975; Larson 1980a, b, c). Little of this literature deals with the juvenile stage. Juvenile rockfishes often use nearshore kelp beds as nursery grounds and, during certain times of the year, are the most abundant members of the kelp-forest fish community (Burge and Schultz 1973). The change from pelagic life to a nearshore, reef-dwelling existence represents a major ecological transition. With so many juvenile rockfish species co-occurring in kelp forests, the potential for competitive interaction is great. Gaining an understanding of these fishes' patterns of resource utilization (e.g., food or space) may be important in assessing the mechanisms that affect their survival.

The purpose of this study was threefold: 1) to investigate the food habits of juvenile rockfishes occurring in a nearshore kelp forest, 2) to determine the extent to which diet differed within and among the various species present, and 3) to compare the relationship between diet and morphology in juvenile and adult forms.

The juveniles of seven rockfish species were studied. The adults of six of these species usually occur nearshore, in association with rock reefs: blue rockfish, *S. mystinus*; black rockfish, *S. melanops*; olive rockfish, *S. serranoides*; copper rockfish, *S. caurinus*; gopher rockfish, *S. carnatus*; and kelp rockfish, *S. atrovirens* (Hallacher 1977; Roberts 1979). Adults of the seventh species, the canary rockfish, *S. pinniger*, occur deeper and usually offshore (Miller and Lea 1972). For purposes of this study, an individual was designated a juvenile upon first appearance in the kelp forest, where fish were usually 25 to 30 mm SL. The fish used in this study generally ranged from 30 to 70 mm SL.

Sebastes mystinus and *S. pinniger* are among the earliest species to recruit, usually appearing as early as April. *Sebastes mystinus* usually occurs in the water column above 6 m while *S. pinniger* occurs on the substrate usually near sand/rock interfaces. *Sebastes caurinus* begins recruiting around late April or May and is found initially among kelp fronds and near the surface. Next to arrive are *S. serranoides* and *S. melanops* which first appear in May and June. Both these species occur mostly in the midwater within the kelp forest. *Sebastes carnatus* usually begins to recruit in late June and July and, like *S. caurinus*, is found initially among kelp fronds at the surface. Both *S. caurinus* and *S. carnatus* move down from the canopy and take positions near the bottom after a couple of months (around June or July for *S. caurinus* and late August or September for *S. carnatus*). The last of these species to recruit is *S. atrovirens*, which begins to appear in late July and August and occurs in the surface kelp canopy.

METHODS AND MATERIALS

Study Site

All observations and samples were taken between

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May 1980 to October 1981 at a rock reef at Arrowhead Point in Stillwater Cove, Carmel Bay, CA (about lat. 36°33.6′N, long. 121°56.3′W). Bottom depths at the study site averaged about 12.5 m below MLLW (mean low low water). The reef was roughly triangular, bounded by sand flats which sloped into deeper water on all but the nearshore side (Fig. 1). The reef substrate was composed of both high and low relief basaltic rock interspersed with areas of coarse, granitic sand and a few patches of worm tubes (*Diopatra* sp.). Stillwater Cove is protected from the prevailing north and northwest swells and winds. However, it is exposed to the most severe southerly storms which commonly occur from October to February.

The rock substrate was covered with an extensive mat of coralline algae and sessile invertebrates. The dominant algal form was the giant kelp, *Macrocystis pyrifera*, which became very thick in the summer months and represented a major structural component of the reef. Except for corallines, understory algae (*Pterogophora californica*, *Cystoseira osmundacea*, and seasonally dense patches of *Desmarestia ligulata*) were relatively sparse and patchy. *Desmarestia* abundance increased in the fall as the surface kelp canopy decreased. Drift algae of several types entered the reef at times and often became a major microhabitat. It usually occurred along the sand/rock interface or in low patches in the interior of the reef.

Field Collections

All fish used for stomach content analysis were collected with a 1 m × 1 m × 1.5 m opening-closing, diver-held net. The net was constructed of 1/8-in stretch-mesh nylon netting on a 1/4-in PVC frame mouth. The mouth of the net was hinged in the middle with tygon tubing. This allowed easy operation by a single diver in close spaces. Collected fish were brought to the surface and the stomachs injected with 10% Formalin[2]. The fish were then preserved whole in 10% Formalin, then washed in freshwater, and stored in 70% ethanol.

The majority of fish collected for gut analysis were taken from June to August of both 1980 and 1981 with some supplemental collections occurring in October and November of 1980. Collections were made during both day and night.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Laboratory Methods

Each fish was blotted dry and weighed to the nearest 0.01 g. The entire visceral mass was removed, and the stomach and intestine were then separated from the remaining viscera. The contents of each stomach were emptied into a small dish and examined under a binocular dissecting scope. Food items were separated by general taxonomic category (e.g., calanoid copepods, zoea larvae, mysid shrimp, etc.). These general categories were used because not all prey items found were in good enough condition to identify to species, thus identifying some items further than others could be misleading. Each category was enumerated by number and percent volume. The percent of the total stomach volume of each prey type was estimated by spreading the contents to a uniform thickness over a background grid and then estimating the area represented by each type. Since contents were spread to an equal thickness, area and volume were considered directly proportional. Digestive state of contents was estimated on a subjective one to five scale (DeWitt and Cailliet 1972). In addition, a subset of each prey type was taken from stomach contents and measured along its longest axis to the nearest 0.005 mm using an ocular micrometer for later estimation of mean sizes of each prey type.

Analytical Methods

A plot of cumulative number of prey types against randomly pooled number of stomachs was constructed for each species in order to assess adequacy of sample sizes. An asymptotic leveling of this type of plot indicates a sufficient sample size. The mean percent by estimated volume (%V) and by number (%N) of each prey type were calculated for each fish species as an average of all values for individual specimens. The mean frequency of occurence (%FO) was also calculated for each prey type in each predator as the number of times the prey type was seen divided by the total of stomachs examined. The importance of each prey type was calculated using the index of relative importance (IRI) described by Pinkas et al. (1971). The IRI used the proportion by amount (%N), volume (%V), and occurrence (%FO) of each prey type (IRI = (%N + %V) × %FO). The diets of the seven species studied were compared using the percent similarity index (PSI) (Whittaker 1952): $PSI = 1 - 0.5 \Sigma pih - pjh$. Where pi and pj are the proportions by IRI of each prey type (h) in the two predators being compared. In calculating

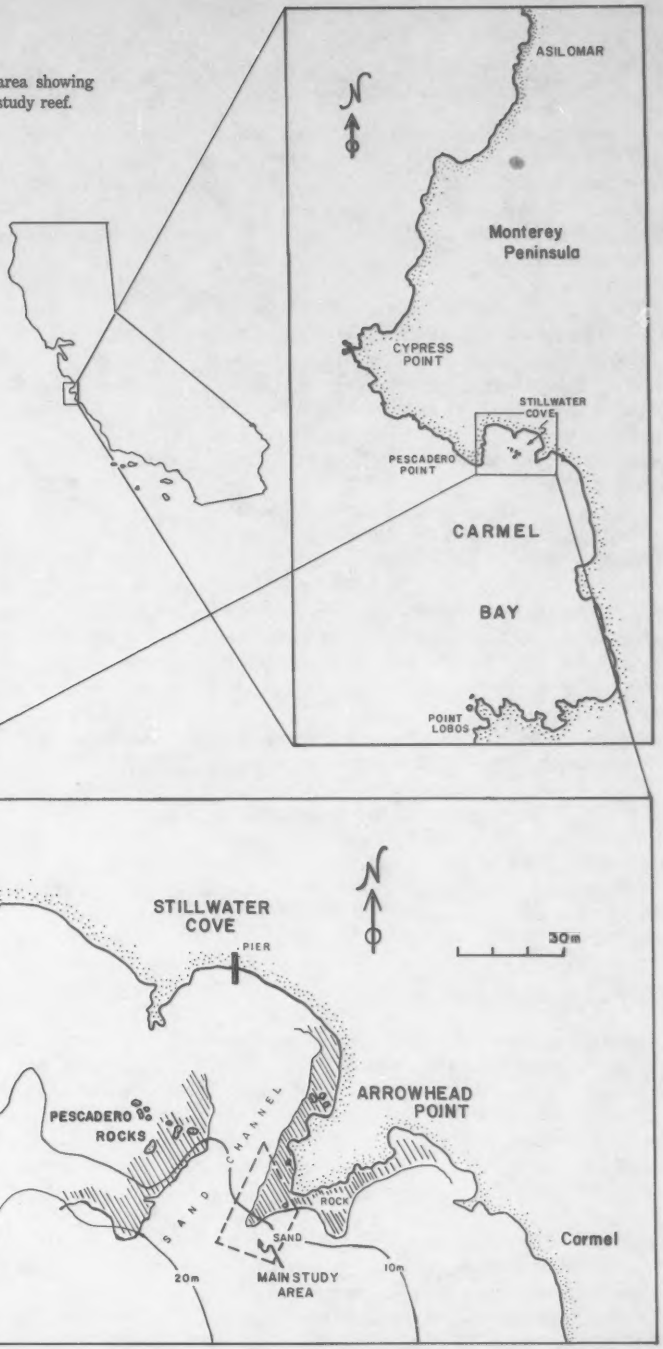

FIGURE 1.—Map of vicinity of sampling area showing Stillwater Cove and the location of the study reef.

overlap values %IRI values were used as the proportion, p.

Morphological Comparison

Several measurements were taken on a subsample of fish of each species covering all sizes encountered in this study. These included standard length, head length, and gape. Mean length of the five gill rakers nearest the angle on the ventral limb of the first gill arch, and the gap between them, were also measured.

The feeding related morphological characteristics chosen for statistical comparison were head length, gape, gill raker length, and gill raker spacing. Gape and gill raker spacing were compared as absolute measurements. Gill raker lengths were standardized to a proportion of head length and head length was standardized as a proportion of standard length for comparison.

Gape was compared using a one-way analysis of covariance (ANCOVA). This analysis regressed the natural log of the gape against the natural log of fish standard length to allow comparison over a range of fish sizes and to achieve linearity (Sokal and Rohlf 1969; Chen 1971). Relative head length, gill raker spacing, and relative gill raker length were compared among species with a Model I, one-way analysis of variance (ANOVA).

Multiple range comparisons were then made between individual species to detect groupings. Regression lines resulting from the ANCOVA were subjected to Newman-Keuls pairwise comparisons. Mean values obtained from ANOVAs were subjected to Student-Newman-Keuls (SNK) multiple range tests. All statistical procedures used followed those presented in Sokal and Rohlf (1969) and Snedecor and Cochran (1980).

Prey Abundance

Qualitative assessment of prey abundances was made from zooplankton tows done in the kelp forest. A standard 0.5 m diameter net with 0.333 μm mesh was used. Tows were done in sets of three, 3 min each: one within 0.5 m of the canopy, one in midwater, and one within 0.5 m of the bottom. These were done during both day and night. Generally, only presence or absence of plankton types was noted, along with relative daytime vs. nighttime differences in abundances. Absolute abundances were not estimated. Zooplankton samples were taken once in mid-June 1980 and once in mid-July 1981. A total of 12 samples were collected.

RESULTS

A total of 265 juveniles of the seven species was examined for stomach content analysis: 27 *S. melanops* (53 to 67 mm SL, $\bar{x}$ = 57.9); 51 *S. serranoides* (44 to 63 mm; $\bar{x}$ = 51.8); 63 *S. pinniger* (28 to 56 mm, $\bar{x}$ = 43.7); 23 *S. mystinus* (46 to 72 mm, $\bar{x}$ = 59.1); 38 *S. atrovirens* (38 to 64 mm, $\bar{x}$ = 47.1); 42 *S. caurinus* (35 to 62 mm, $\bar{x}$ = 48.7); and 21 *S. carnatus* (33 to 65 mm, $\bar{x}$ = 44.4). An often cooccuring cogener of *S. carnatus*, *S. chrysomelas*, was not found during this study.

Diet Analysis

The cumulative prey type curves versus number of stomachs examined leveled off asymptotically, indicating that sample sizes for all species were sufficient to characterize their food arrays. All species were found to be zooplanktivores, consuming both open water and substrate-associated prey. Open water prey, which mainly float free in the water column, consisted mostly of juvenile copepods, zoea, and juvenile spionid polychaetes, while substrate-associated prey, which were generally found directly associated (<0.5 m away) with a physical structure (rock, kelp, etc.), consisted mainly of gammarid amphipods, mysid and caridean shrimp, and two species of isopod (Table 1).

A wide variety of prey sizes were encountered (Table 2). Prey found in open water, such as calanoid and harpacticoid copepods, zoea, and larvaceans, were mostly < 1 mm in length, whereas substrate-associated prey, such as amphipods and decapods, were 3 to 4 mm or larger.

Mean number of prey items and prey taxa per individual were highly variable within and among species (Table 3). As would be expected, species which fed on small open water prey had higher numbers of prey per stomach. Conversely, those species which fed on large substrate-associated prey, which were often large enough to fill a stomach with a single prey item, had much lower numbers of prey items per stomach.

Sebastes mystinus fed mainly on the larvacean *Oikopleura* sp., with high occurrence of copepods, zoea, and juvenile polychaetes (Fig. 2). They had the most cosmopolitan diet and the highest intraspecific variability of prey types (a mean of almost six different prey types per individual) (Table 3). Because its diet was composed mainly of small open water prey, this species also had the highest mean number of prey items per individual.

Sebastes serranoides and *S. melanops* had very

TABLE 1.—Taxa of prey identified in the stomachs of juvenile rockfish; names in all-capitals are categories used in stomach content analysis. (?) signifies incomplete or unsure identification. Microhabitat associations: OW = open water prey, S = substrate oriented prey.

Prey type			Open water or substrate association
Algae			
Mostly reproductive *Cystociera osmundacea*			S
Occasional pieces of *Macrocystis* fronds			
Invertebrates			
Molluscs	- *Macoma* sp.		S
Copepods	- CALANOIDS: unidentified juveniles		OW
	HARPACTICOIDS: unidentified juveniles		OW/S
OSTRACODS	- Unidentified		OW
POLYCHAETES	- larval/juvenile Spionidae		OW
Cirripidea	- unidentified BARNACLE LARVAE		OW
ISOPODS	- *Dimonella globera*; *Idothea resicata*		S
Amphipods	- GAMMARIDS:	*Aoroides columbiana*	S
		Ampithoe sp.	
		Batea transversa	
		Najna kitmata (?)	
	CAPRELLIDS:	*Caprella* sp.	S
		Unidentified Protocerid	
	HYPERIIDS:	Unidentified	S
MYSIDS	- *Acanthomysis* sp.; *Neomysis* sp.		S
Decapods	- SHRIMP:	*Heptocarpus* sp.	S
		Hippolyte sp. (?)	
	ZOEA LARVAE: unidentified decapods and brachyurans		OW
	ANOMURANS: unidentified JUVENILE HERMIT CRAB		S
Larvaceans	- *Oikopleura* sp.		OW
FISH			
unidentified hard parts			S
unidentified fish eggs			OW

TABLE 2.—Mean (±95% confidence interval) sizes of individuals of the nine major prey types of juvenile rockfishes. Measured items were taken from stomach samples.

Species	Size (mm)		
	N	$\bar{x}$	95% C.I.
Open water prey			
Oikopleura sp.	50	0.69	0.04
Harpacticoid copepods	50	0.88	0.05
Calanoid copepods	50	0.96	0.03
Juvenile polychaetes	35	1.47	0.71
Zoea larvae	50	1.63	0.11
Substrate-associated prey			
Mysids	35	3.48	1.16
Gammarid amphipods	35	4.01	0.77
Isopods	30	4.29	0.89
Caridean shrimp	30	13.95	1.47

similar diets (Fig. 2, Table 4). Both species ate mainly open water prey: calanoid copepods, harpacticoid copepods, and zoea larvae in order of importance. These species also showed fairly high intraspecific diet variability—5.3 and 4.4 prey taxa per individual for *melanops* and *serranoides*, respectively.

The two species which showed major microhabitat shifts (Carr 1983), *S. caurinus* and *S. carnatus*, also showed large dietary changes. While in the canopy (generally <45 mm in SL), *S. caurinus* ate predominantly calanoid copepods, with harpacticoids and zoea also eaten fairly consistently (Fig. 2). However, after moving out of the canopy and down to the bottom near kelp stipes and rocks, its diet shifted to primarily caridean shrimp, with gammarid amphipods being the second most important prey (Fig. 2). *Sebastes carnatus* showed much the same type of dietary shift accompanying its large habitat shift. While in the canopy, smaller *S. carnatus* ate nearly exclusively calanoid copepods (92% of the diet), while large individuals, which were found on the bottom, fed on caridean and mysid shrimp and isopods (Fig. 2). This marked change in diet can also be seen in Table 4. Within each of these species, the diet similarity between size classes was low. However, similarities between the two species within each size class was quite high.

Sebastes atrovirens was found in the kelp canopy and among kelp throughout all depths during the entire study (Carr 1983). This species fed mainly on gammarid amphipods, with calanoid and harpacticoid copepods and mysid shrimp also being very

TABLE 3.—Mean (±95% confidence interval) number of prey items and prey taxa per stomach and total number of prey types for the seven species of juvenile rockfishes.

Species	Items			Taxa		S
	N	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.	Total
Open water predators						
Sebastes mystinus	23	142.6	74.9	5.8	0.4	13
S. caurinus (<45 mm)	17	136.4	64.7	3.4	0.7	8
S. carnatus (<45 mm)	12	101.4	79.6	1.9	0.7	5
S. serranoides	50	100.2	33.5	4.4	1.7	9
S. melanops	27	87.0	31.2	5.3	2.3	8
Substrate-oriented predators						
S. pinniger	59	35.5	18.3	4.3	1.6	15
S. atrovirens	33	34.9	20.3	2.2	0.4	8
S. caurinus (>45 mm)	21	2.5	1.3	1.5	0.3	9
S. carnatus (>45 mm)	11	2.3	1.2	1.6	0.7	5

TABLE 4.—Percent similarity (PSI) overlap values of juvenile rockfish diets. Proportions used for calculations are %IRI.

	serranoides	*melanops*	*mystinus*	*caurinus* <45 mm	*carnatus* <45 mm	*pinniger*	*atrovirens*	*caurinus* >45 mm	*carnatus* >45 mm
Sebastes serranoides	—	0.787	0.455	0.874	0.602	0.653	0.389	0.091	0.090
S. melanops		—	0.402	0.732	0.516	0.734	0.318	0.094	0.019
S. mystinus			—	0.384	0.127	0.458	0.239	0.097	0.043
S. caurinus (<45 mm)				—	0.668	0.573	0.427	0.185	0.204
S. carnatus (<45 mm)					—	0.297	0.259	0.043	0.034
S. pinniger						—	0.468	0.174	0.169
S. atrovirens							—	0.218	0.258
S. caurinus (>45 mm)								—	0.634
S. carnatus (>45 mm)									—

important in their diet (Fig. 2). Thus, this species' diet was similar to most other species (Table 4).

Sebastes pinniger had a very diverse diet (highest number of overall prey taxa found; Table 3). Individuals were found mainly over sand areas and the sand/rock interface at the edge of the kelp forest, generally within a few meters of the bottom. This species' diet consisted mainly of copepods and zoea larvae (open water prey), but gammarid amphipods and mysid shrimp (substrate-associated prey) were also important (Fig. 2).

Figure 2 shows that these seven species can be split into two basic categories: open water and substrate-associated predators (this categorization can also be seen in microhabitat differences [Carr 1983]). Open water predators—*S. melanops*, *S. mystinus*, *S. serranoides*, and small *S. caurinus* and *S. carnatus*—are those that ate mainly copepods and zoea larvae. Substrate-oriented predators—*S. atrovirens* and larger *S. caurinus* and *S. carnatus*—are those that ate predominantly amphipods and decapods. *Sebastes pinniger* is intermediate between these categories. Its microhabitat and behavior are that of a substrate-associated predator, but its diet is more similar to the open water predators (Table 4).

Prey Distribution

Midwater organisms such as copepods, zoea larvae, and polychaetes were very abundant in all parts of the water column. Calanoid copepods were the most abundant type during the day at all depths, while both calanoids and harpacticoids were very abundant at night. Amphipods, mysids, caridean shrimp, and isopods were very abundant in and around all substrate types (kelp canopy, stipes, rocks, and drift algae). Isopods and amphipods were most abundant in the canopy and stipes, while amphipods, mysids, and carideans were more often abundant near rock and drift algae and around kelp holdfasts. These invertebrates remained near substrate during the day, moving farther away at night.

Morphological Comparisons

ANOVAs of relative head length, relative gill raker length, and gill raker spacing among species were all significant at the $P < 0.001$ level (Table 5). Generally, the open water and substrate-associated classifications also held true for groupings by morphology.

In general, open water predators had smaller heads and larger gill rakers. *Sebastes mystinus*, *S.*

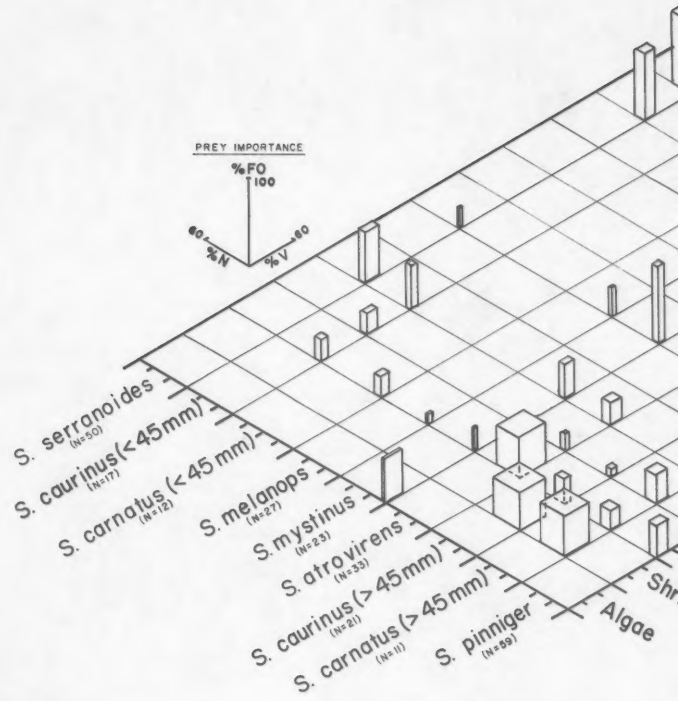

FIGURE 2.—Three dimensional trophic spectrum of juvenile rockfish diets. %N and %V are
prey type's i

%V are the horizontal axes with %FO on the vertical axis. Size of each box is equivalent to each ype's importance.

TABLE 5.—Results of Student-Newman-Keuls multiple range comparisons on head length and gill raker length and spacing of juvenile rockfishes (*Sebastes*). Numbers in parentheses are significance levels of analyses of variance (ANOVA).

Relative head length ($P < 0.0001$)
Groupings at $\alpha = 0.05$ level (mean head lengths)

mystinus	*serranoides*	*melanops*	*atrovirens*	*caurinus*	*pinniger*	*carnatus*
0.3368	0.3620	0.3660	0.3808	0.3882	0.3890	0.3908

Relative gill raker length ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean raker lengths)

carnatus	*caurinus*	*atrovirens*	*serranoides*	*pinniger*	*mystinus*	*melanops*
0.1008	0.1070	0.1165	0.1185	0.1222	0.1296	0.1322

Gill raker spacing ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean spacing)

pinniger	*melanops*	*atrovirens*	*carnatus*	*mystinus*	*caurinus*	*serranoides*
0.226	0.234	0.238	0.248	0.262	0.312	0.316

serranoides, and *S. melanops*, which all have relatively long, slender bodies, had significantly smaller heads than *S. caurinus*, *S. carnatus*, and *S. pinniger* (Table 5). *Sebastes mystinus* and *S. melanops* also had significantly longer gill rakers than *S. caurinus* and *S. carnatus*, with *S. serranoides* having intermediate length rakers. *Sebastes atrovirens* was relatively intermediate in both measurements, but tended to be more like the predators with larger heads and shorter gill rakers. Groupings for gill raker spacing were less distinct. The open water/substrate-associated classifications also broke down with this measurement. *Sebastes pinniger*, *melanops*, and *atrovirens* had more closely spaced rakers, while *S. caurinus* and *serranoides* had the widest spaced rakers. *Sebastes mystinus* had an intermediate value (Table 5). Regression lines obtained from the ANCOVA showed that gape grew isometrically with length in all seven species, but that there were significant differences in the size of gape relative to body size among the species (Table 6). The slopes of the lines of ln (gape) on ln (SL) were all statistically indistinguishable from unity, but the intercepts did show a significant difference ($P < 0.001$, ANCOVA). Much of this significant difference was likely due to *S. caurinus*, which had a much larger mouth than the other species. *Sebastes serranoides* also had a fairly large mouth. All other species had very similar-sized mouths (Table 6).

TABLE 6.—Results of the one way analysis of covariance (ANCOVA) performed on regressions of ln (gape) versus ln (SL) of juvenile rockfishes.

Regression statistics

Species	Slope	Intercept	*r*
Sebastes caurinus	0.6745	−0.4173	0.8259
S. serranoides	0.8332	−1.2024	0.8363
S. pinniger	0.9876	−1.6759	0.9640
S. melanops	0.9761	−1.7070	0.9614
S. mystinus	0.9555	−1.7470	0.9224
S. carnatus	1.0482	−1.8439	0.9652
S. atrovirens	1.0561	−2.0053	0.9661

ANCOVA statistics

	MSnum	df	MSdenom	df	*F*	*P*
Slope	0.01	7	0.0057	155	1.76	NS
Intercept	0.16	6	0.039	161	40.68	$P < 0.001$

DISCUSSION

Many species of fish change diet as they grow (Ross 1978; MacPherson 1981). This may be because of changes in habitat, thus changing available food sources, or it may simply be a functional response to changes in fish size and/or metabolic needs. Although there are dietary differences between the juveniles and adults of the species studied here, their foraging patterns and habitats are very much the same.

Species who were water column feeders as juveniles remain water column feeders as adults. Juvenile *S. serranoides* ate primarily copepods and zoea larvae (Hobson and Chess 1976; this study). Adults also feed in the water column, eating primarily small fish and euphausiids (Love 1978). Juvenile *S. melanops* fed in the open water (on copepods), as do the adults, which eat small fish, euphausiids, and polychaetes (Hallacher 1978; Roberts 1979). This trend also holds for *S. mystinus*. Juveniles foraged in the water column, mostly on *Oikopleura* and copepods. Adults also aggregate and feed in the open water, but eat mostly tunicates and crustaceans (Hallacher 1977; Roberts 1979).

The ontogenetic similarity in foraging was also seen in substrate-oriented feeders. Juvenile *S. atrovirens* ate mostly large, demersal, gammarid amphipods. However, copepods ranked second in their diet, presumably because of small individuals feeding in the open water below the kelp canopy. Adults of this species feed on amphipods, shrimp, and crabs which can be either demersal or free swimming (Quast 1968; Hobson and Chess 1976; Roberts 1979). Small juvenile *S. caurinus* and *S. carnatus* fed in the open water, while larger juveniles foraged demersally. The adults of these species also feed demersally. *Sebastes carnatus* is known to eat juvenile rockfish, ophiuroids, and crustaceans (Hallacher 1977; Roberts 1979), while adult *S. caurinus* eat mostly brachyurans and shrimp (Prince 1975; Prince and Gotshall 1976). Juveniles also seem to exhibit the same microhabitat preference as adults. *Sebastes serranoides, mystinus,* and *melanops* were found mainly in the midwater, while *S. caurinus, carnatus,* and *atrovirens* were generally seen to associate more closely with some physical substrate (kelp plants, rocks, etc.) (Carr 1983; pers. obs.). Thus, in these species it seems that once an individual has survived its life as a pelagic larva and entered the kelp forest, it assumes the general habitat and foraging characteristics of an adult.

Sebastes pinniger was the only species which showed different foraging patterns between juveniles and adults. Juvenile *S. pinniger* were generally found close to the bottom over sand or in association with the rock/sand interface at the edge of the reef (Carr 1983; pers. obs.) while adults occur higher in the water column in deep water offshore. Juveniles fed demersally on copepods over sand and drift algae very near the kelp forest. Adults feed in the water column on euphausiids and small fish (Phillips 1964). Recently, adults have been found to be more demersal feeders than other offshore rockfish (Brodeur 1982).

In assessing the mechanisms which might lead to the observed diet differences, several factors must be considered, such as prey distribution and abundance, prey availability, predator morphology, prey and predator activity patterns, and predator distribution.

Qualitative analysis of plankton samples, combined with underwater observations, showed that plankton were very abundant. Although the diel behavior patterns of shallow, inshore zooplankton are highly variable with respect to specific habitats, species, seasons, and latitudes, the patterns of plankton distribution observed were quite comparable with reported accounts in kelp forests (Hobson and Chess 1976; Coyer 1979; Hammer 1981).

Predator morphology is an important factor determining prey size in planktivorous fish. Certain features distinguish water column foraging fish, such as long, slender bodies, sharp head profiles, fine dentition on jaws and pharyngeal bones, and long, closely spaced gill rakers (Yasuda 1960; Davis and Birdsong 1973). Of the seven species studied, the water column feeders—*S. mystinus, S. serranoides,* and *S. melanops*—had smaller heads with longer gill rakers.

Water column foragers and substrate-associated foragers could be separated by both morphology and prey size. The water column foragers—*S. mystinus, S. serranoides,* and *S. melanops*—all had relatively long, slender bodies, small heads, and long gill rakers. This agrees with predictions, especially since the adults of these species are also water column foragers. Water column feeders also ate substantially smaller prey than did substrate predators (see Figure 2, Table 2). The substrate-associated feeders—*S. caurinus, S. carnatus,* and *S. atrovirens,* which ate larger prey—all had stouter bodies, larger heads, and shorter, less ornamented gill rakers.

Juveniles of *S. pinniger* were somewhat intermediate in feeding morphology. Their heads were large and stout, indicative of substrate-oriented feeding. However, they had long, thin bodies and long, fairly closely spaced gill rakers, which is indicative of water column foraging, as is displayed by adults. This intermediate situation may be indicative of the fact that *S. pinniger* may go through a second ecological transition from a reef-dwelling, substrate-associated juvenile form back to a more pelagic offshore situation as an adult.

Differing diel patterns can be one way for co-occurring predators to exploit similar resources while keeping interspecific interactions low (Keast and Webb 1966; Schoener 1974; Bray and Ebeling 1975). In zooplanktivores diel patterns of both predators and prey are important (Hobson and Chess 1976; Robertson and Howard 1978). Most juveniles were active only during the day, with the possible exceptions of *S. pinniger* and *S. serranoides* (Singer 1982). This was also reflected in greater stomach fullness of most species in the afternoon and early evening, indicating diurnal feeding patterns (Singer 1982). Plankton abundances were high during both day and night. However, more species were found in the water column at night. Thus, while some of these fish could do well feeding at night, daytime abundances of food seemed sufficient for their needs. Juveniles were indeed found to be most active and to feed most frequently during daylight hours, but intraspecific variability was high (Singer 1982).

Digestion was fairly slow in all species, taking at least 9 to 12 h for a full stomach of food to be half digested (Singer 1982). Together, these indicate that individuals may not need to feed every day and that both within and among species these populations may feed with a high degree of asynchrony (Singer 1982).

Do the observed differences in diets suggest interspecific competition? Central to competition theory is the presumption that individuals or populations use the same or a very similar resource and that this resource is in short supply (Pielou 1975; Pianka 1978). Abundances of all types of plankton used by these fishes are high. The fact that individuals can probably fill their stomachs in a very short time period (Singer 1982) indicates that their needs are easily met. This suggests that competition for food does not play an important role in the foraging patterns of these species. Other factors, such as the lack of observed aggressive interactions within or among the species studied in over 1,100 min of in situ feeding observations, high overlap in time of feeding, generally low similarity of diet, and high intraspecific variability within foraging patterns suggest there is little food competition (Singer 1982).

Similarly, available evidence suggests little competition for space among juveniles (Carr 1983). When juveniles enter the kelp forest system, they immediately occupy habitats characteristic of adults; thus, habitat preference may be under some genetic control. Close spatial co-occurrence with the absence of agonistic interactions suggests that competition for space is minimal in these fish. Also, within the kelp forest studied, juvenile rockfishes are the predominant planktivores, and are thus relatively free of other possible competitors. Other kelp forest planktivores such as *Chromis punctipinnis*, *Oxyjulius californica*, and *Brachyistius frenata* are present, but in very low numbers, and often only for short periods of time.

Thus, the differences in diet seen in this study appear to be the consequences of these species exploiting localized food resources encountered in different microhabitats. Competition for food does not seem to be a strong ecological influence among these juveniles.

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Literature Cited

BRAY, R. N., AND A. W. EBELING.
1975. Food activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forest off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BRODEUR, R. D.
1982. Food habits, dietary overlap and gastric evacuation rates of rockfish (Genus *Sebastes*). M.S. Thesis, Oreg. State Univ., Corvallis, 98 p.

BURGE, R. T., AND S. A. SHULTZ.
1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

CARR, M. A.
1983. Spatial and temporal patterns of recruitment of young-of-the-year rockfishes (genus *Sebastes*) into a Central California kelp forest. M.A. Thesis, San Francisco State Univ., San Francisco, 122 p.

CHEN, L. C.
1971. Systematics, variation, distribution, and biology of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Univ. Calif. Press, Berkeley, 107 p.

COYER, J. A.
1979. The invertebrate assemblage associated with *Macrocystis pyrifera* and its utilization as a food source by kelp forest fishes. Ph.D. Thesis, Univ. Southern California, Los Angeles, 364 p.

DAVIS, W. P., AND R. S. BIRDSONG.
1973. Coral reef fishes which forage in the water column, a review of their morphology, behavior, ecology and evolutionary implications. Helgo. Wiss. Meersunters. 24:292-306.

DELACEY, A. C., K. R. HITZ, AND R. L. DRYFOOS.
1964. Maturation, gestation and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Wash. State Dep. Fish. Res. Pap. 2(3):51-67.

DEWITT, F. A., JR., AND G. M. CAILLIET.
1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). Copeia 1972:868-871.

HALLACHER, L. E.
1977. Patterns of space and food use by inshore rockfishes (Scorpaenidae; *Sebastes*) of Carmel Bay, California. Ph.D. Thesis, Univ. California, Berkeley, 119 p.

HAMMER, R. M.
1981. Day-night differences in the emergence of demersal zooplankton from a sand substrate in a kelp forest. Mar. Biol. (Berl.) 62:275-280.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters

near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

KEAST, A., AND D. WEBB.
1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23:1845-1874.

LARSON, R. J.
1980a. Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae; *Sebastes*). Mar. Biol. (Berl.) 58:111-122.
1980b. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes*. Mar. Biol. (Berl.) 58;123-132.
1980c. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50:221-239.

LOVE, M. S.
1978. Aspects of the life history of the olive rockfish, *Sebastes serranoides*. Ph.D. Thesis, Univ. California, Santa Barbara, 183 p.

MACPHERSON, E.
1981. Resource partitioning in a Mediterranean demersal fish community. Mar. Ecol. Prog. Ser. 4:183-193.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish. Game, Fish Bull. 158, 137 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

PIANKA, E. R.
1978. Evolutionary ecology. Harper and Row, N.Y., 397 p.

PIELOU, E. C.
1975. Ecological diversity. Wiley-Interscience, N.Y., 165 p.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

PRINCE, E. D.
1975. Pinnixid crabs in the diet of young-of-the-year copper rockfish (*Sebastes caurinus*). Trans. Am. Fish Soc. 104:539-540.

PRINCE, E. D., AND D. W. GOTSHALL.
1976. Food of the copper rockfish, *Sebastes caurinus* Richardson, associated with an artificial reef in South Humboldt Bay, California. Calif. Fish Game 62:274-285.

QUAST, J. C.
1968. Observations of the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in Southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

ROBERTS, D. A.
1979. Food habits as an ecological partitioning mechanism in the nearshore rockfishes (*Sebastes*) of Carmel Bay, California. M.A. Thesis, San Francisco State Univ., San Francisco, 74 p.

ROBERTSON, A. I., AND R. K. HOWARD.
1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. Mar. Biol. (Berl.) 48:207-213.

ROSS, S. T.
1978. Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Fish. Bull., U.S. 76:225-234.

SCHOENER, T. W.
1974. Resource partitioning in ecological communities. Science (Wash., D.C.) 185:27-39.

SINGER, M. M.
1982. Food habit and activity patterns of juvenile rockfishes (*Sebastes*) in a central California kelp forest. M.A. Thesis, Moss Landing Marine Laboratories, Moss Landing, CA, 75 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames, 507 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principals and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

WESTRHEIM, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the Northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

WHITTAKER, R. H.
1952. A study of the summer foliage insect communities in the Great Smokey Mountains. Ecol. Monogr. 22:1-44.

YASUDA, F.
1960. The relationship of the gill structure and food habits of some coastal fishes in Japan. Rec. Oceanogr. Works Jpn. New Ser. 5(2):139-152.

RADIO TRACKING THE MOVEMENTS AND ACTIVITIES OF HARBOR PORPOISES, *PHOCOENA PHOCOENA* (L.), IN THE BAY OF FUNDY, CANADA

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ABSTRACT

Eight harbor porpoises were radio-tagged (172-173 MHz) and released in the western Bay of Fundy between August 1981 and August 1983. The duration of contact with radio-tagged animals ranged from 0.3 to 22.4 days. One harbor porpoise was tracked for 22.4 days and utilized a home range area of 210 km^2. In all observed cases, the movement of radio-tagged porpoises coincided with the direction of tidal flow in the major channels and passages of the region. Analysis of 39.2 hours of ventilation sequences revealed that radio-tagged porpoises were relatively inactive from midnight until 0600 and more active during other periods.

This report documents the results of a study on the movements and activities of radio-tagged harbor porpoises, *Phocoena phocoena*, in the Bay of Fundy, Canada. The primary objective of this research was to determine the home ranges of individual harbor porpoises during the summer months. The study also provided insights into the behavior and activities of radio-tagged animals.

Studies of cetacean home ranges often rely on resightings of tagged or naturally marked animals (Irvine et al. 1981; Bigg 1982; Dorsey 1983). These methods are of limited value if individual animals travel outside the area under observation and may result in underestimation of the utilized range. A more effective means of estimating home range area is to monitor the movements of radio-tagged individuals (McDonald et al. 1979). Several recent studies have successfully employed radio-tracking techniques in field studies of cetacean species (see review by Leatherwood and Evans 1979). Notable among these are investigations of *Delphinus delphis* by Evans (1971), of *Tursiops truncatus* by Irvine et al. (1981), and of *Lagenorhynchus obscurus* by Würsig (1982).

In a preliminary study of harbor porpoise movements (Gaskin et al. 1975), we demonstrated that radio-tracking techniques could be successfully applied to this species. Although this initial research was promising, we felt that the transmitters available at that time were too large to be carried by these small porpoises (see Watson and Gaskin 1983). The recent development of smaller transmitters and the continuing availability of live porpoises from herring weirs (Smith et al. 1983) have enabled us to undertake the present study.

METHODS

The study area encompases Passamaquoddy Bay, the channels and passages around Deer Island, and waters further offshore to Grand Manan Island (Fig. 1). During the summer, mean monthly water temperatures for the upper 25 m of the water column range from 6.4° in June to 11.0°C in September (Bailey et al. 1954). The oceanography of the region is dominated by large semidiurnal tides, which have a mean amplitude of 5.5 m at North Head, Grand Manan (Anonymous 1982). The large tides generate strong currents, with velocities reaching a maximum of 2.4 m/s in Letite Passage (Forrester 1960). Further information regarding the oceanography of the region may be found in Smith et al. (1984).

Harbor porpoises were seined from herring weirs (Smith et al. 1983), placed on a sheet of open cell foam, sexed, and measured. The porpoises were liberally sprinkled with seawater throughout the tagging procedure to prevent overheating. Two 0.64 cm diameter holes were bored through the dorsal fin with a laboratory cork borer, cleansed in alcohol prior to use. The holes were immediately cold-cauterized with a histological freezing spray.

Transmitters were attached to the dorsal fin with two 0.64 cm diameter stainless steel bolts, each covered with a thin sleeve of teflon (see Figure 2). A thin, neoprene-lined plastic plate was placed between the transmitter and dorsal fin and an identical plate was positioned on the opposite side of the

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FIGURE 1.—The harbor porpoise study area with place names mentioned in text. The inset shows the study area in relation to the rest of the Bay of Fundy.

fin. The teflon-covered bolts, passed through the transmitter and plastic plates, were fastened with corrodable, low grade steel nuts.

The radio transmitters measured 3.2 × 3.8 × 6.0 cm and weighed about 170 g in air (Model 4-A, Telonics,[2] Mesa, AZ). The transmitting antennae consisted of 43 cm semiflexible whips, designed specifically for use with marine mammals.

Transmitted VHF signals (172-173 MHz) consisted

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

of 20-60 ms pulses at intervals of 0.4 s. Lithium batteries provided a maximum power output of 0.75 mW and an expected transmitting life of 1.6-6.0 mo. The maximum transmitting range across open water was about 15-20 km.

We used a Telonics TR-2 telemetry receiver with a two-element, hand-held directional antenna. The approximate direction of the transmitter was determined by rotating the antenna and noting the strongest signal. A digital data processor (Telonics TDP-2) provided a visual display of signal strength.

The position of a tagged porpoise was determined either by tracking the animal until visual contact was established, or by triangulation from shore. In the latter method, the receiving system was moved along the shore, and signal bearings at two or more locations were noted. The intersection point of these bearings was then used to approximate the position

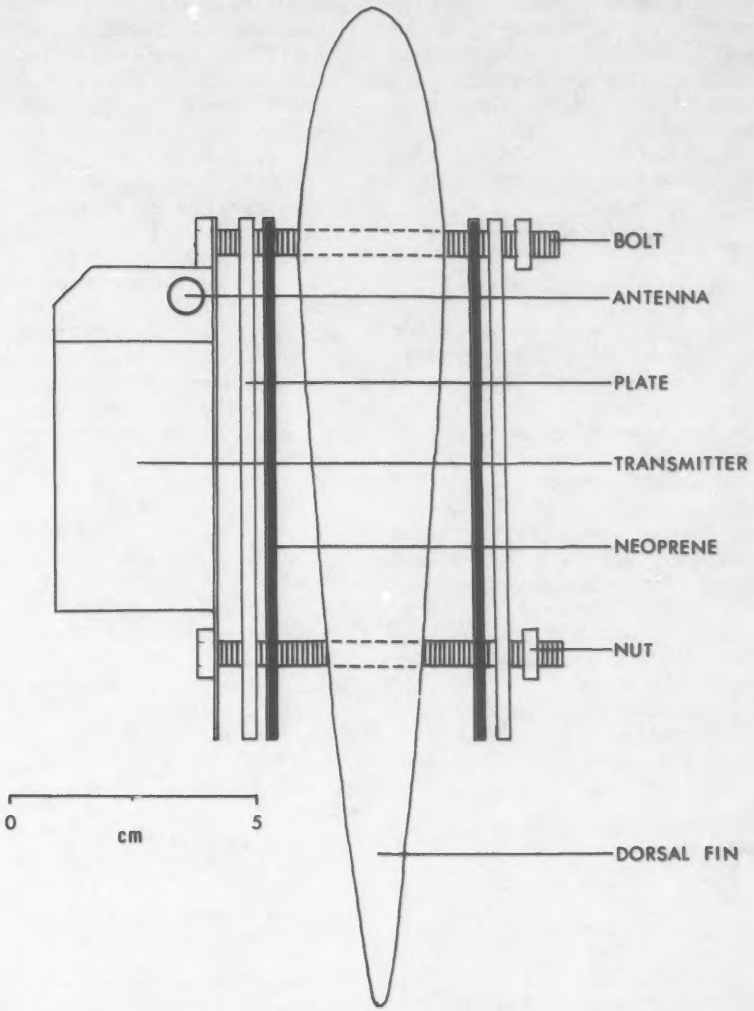


FIGURE 2.--The transmitter package used in radio-tracking studies of harbor porpoises in the Bay of Fundy. The bolts attaching the transmitter to the dorsal fin were covered by thin teflon sleeves.

of the porpoise. To ensure bearing accuracy, a series of readings were taken at each location, and the average used in triangulation (Springer 1979). Each sighting or radio location was assigned to a 1 km grid square of the Universal Transverse Mercator System. Derived radio locations were discarded if the triangulation could not place a porpoise within a 1 km square; the time elapsed between fixes and bearing error (±5°) precluded more precise estimation. Positional data were collected at least once a day, but usually on a more frequent basis.

The radio signal was received only when the transmitting antenna was exposed, allowing the duration of both submergence and surface periods to be recorded. Such ventilation data were collected on an opportunistic basis throughout the tracking period of each porpoise.

A detailed analysis of the methods used in this study is presented in Read and Gaskin (1983).

RESULTS

Movements

Eight harbor porpoises were released carrying transmitters over the course of the study (Table 1). During the attachment procedure, porpoises were out of the water for a mean of 6.6 min (SD ± 1.4, n = 8), during which time most animals remained fairly still. Only two porpoises exhibited any trauma while being handled; RT-5 vomited briefly, and RT-7 (a 110 cm calf) repeatedly lashed its flukes. The latter porpoise appeared momentarily disoriented when returned to the water, but quickly resumed swimming and surfacing normally after being joined by a larger porpoise. The larger animal, presumably the calf's mother, had also been trapped in the weir, but escaped overnight and remained in the vicinity until the calf's release.

Duration of radio contact ranged from 0.30 (RT-5) to 22.4 d (RT-2), with a mean of 5.1 d (SD ± 7.1, n = 8). In some instances, loss of radio contact may have been due to the premature release of the transmitter package. The rear bolt attaching the transmitter to the dorsal fin of RT-3 was missing when the porpoise was photographed 5 h before signal loss occurred. The radio signals of RT-3 and RT-7 were being monitored when contact was lost, and in both cases termination of the signal was abrupt, a pattern compatible with the hypothesis of transmitter loss. In our limited observations of radio-tagged porpoises (see below), we did not see any evidence of displacement of the transmitter package (Irvine et al. 1982).

TABLE 1.—Data summary for harbor porpoises radio-tagged and released in the western Bay of Fundy.

Porpoise code	Length (cm)	Sex	Frequency (MHz)	Date of Release	Duration of contact (d)
RT-1	132	M	173.350	05 08 81	3.05
RT-2	119	M	173.550	20 08 81	22.4
RT-3	145	M	173.500	29 07 82	5.32
RT-4	131	F	173.100	31 08 82	3.16
RT-5	114	M	173.000	31 08 82	0.30
RT-6	116	M	173.700	01 09 82	2.72
RT-7	110	M	173.650	03 09 82	1.83
RT-8	114	M	172.600	09 08 83	2.25

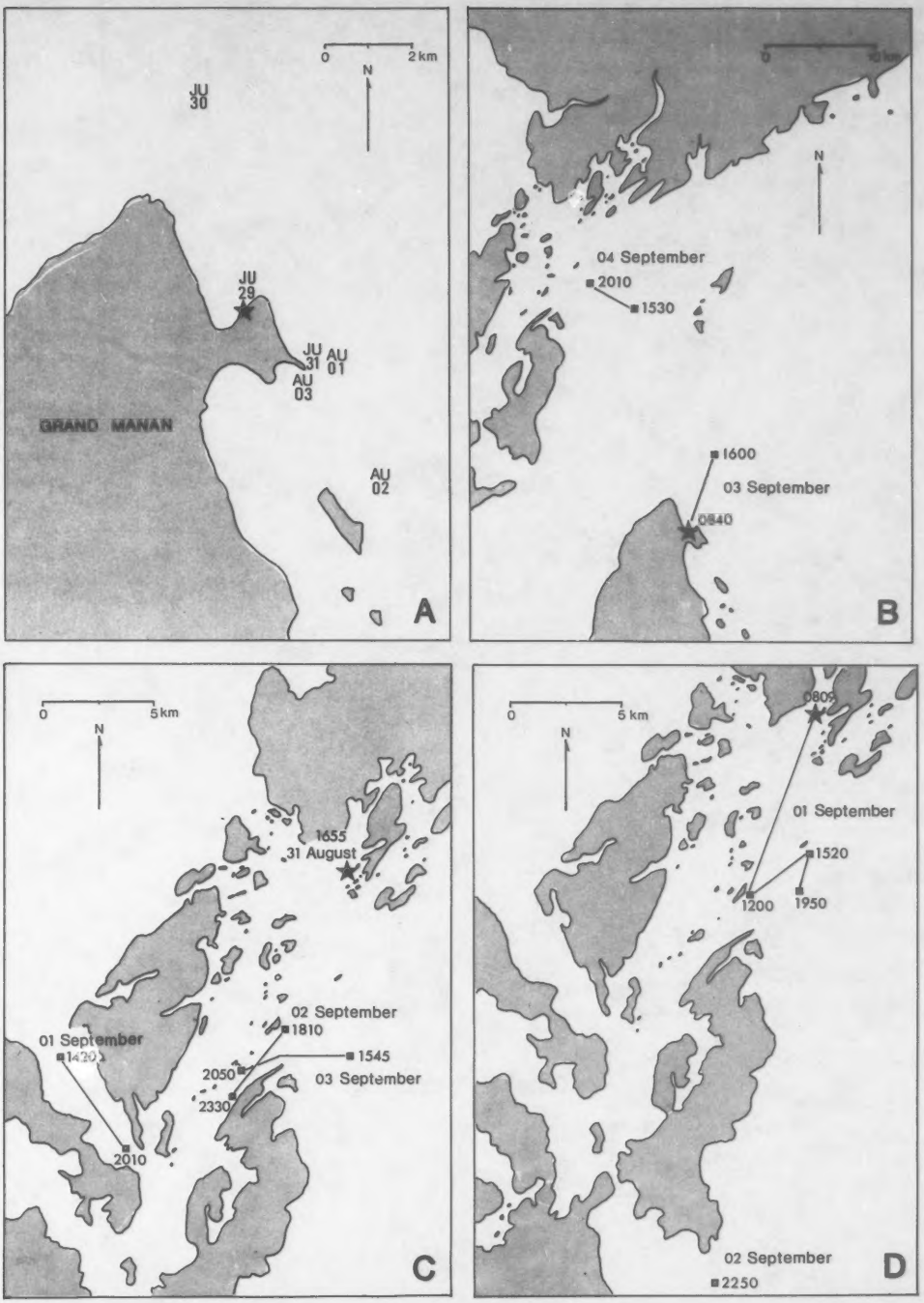
Over the course of the study, three porpoises were released from the same weir in Whale Cove, Grand Manan. Attempts to relocate RT-1, the first porpoise released in Whale Cove, were frustrated by fog and heavy seas which persisted for the entire 3-d tracking period. In addition, the shoreline configuration of northern Grand Manan prevented accurate triangulation. However, the strength and direction of the signal received from shore indicated that the porpoise remained in the vicinity of northern Grand Manan until signal loss occurred. The movements of the other two porpoises released in Whale Cove (RT-3 and RT-7) are illustrated in Figure 3A and B.

On 30 August 1982, four porpoises were reported trapped in a weir in Back Bay, mainland New Brunswick. A female (RT-4), accompanied by a 101 cm calf, and a young male (RT-5) were released on 31 August. The remaining porpoise, another young male (RT-6), was tagged and released the following day. RT-4 and RT-5 remained together for at least 7 h, after which contact was lost with RT-5. The movements of RT-4 and RT-6 are depicted in Figure 3C and D.

The longest tracking sequence recorded in this study was that of RT-2, released near St. Andrews, mainland New Brunswick. This porpoise spent the majority of its 22-d tracking period within Passamaquoddy Bay, although occasional excursions were made to the east of Deer Island (Fig. 4). The home range of RT-2, calculated using the convex polygon method, was about 210 km^2 (excluding land masses).

RT-8, the only porpoise to be radio-tagged in 1983, travelled from its release point in northern Passamaquoddy Bay to West Quoddy in about 48 h. Logistical constraints prevented more precise determination of the movements of this animal.

FIGURE 3.—Movements and positions of radio-tagged harbor porpoises in the Bay of Fundy. The release point of each porpoise is indicated by a star. A) Position of porpoise RT-3 at 1200 of each day of tracking period; B) Movements of porpoise RT-7; C) Movements of porpoise RT-4; D) Movements of porpoise RT-6.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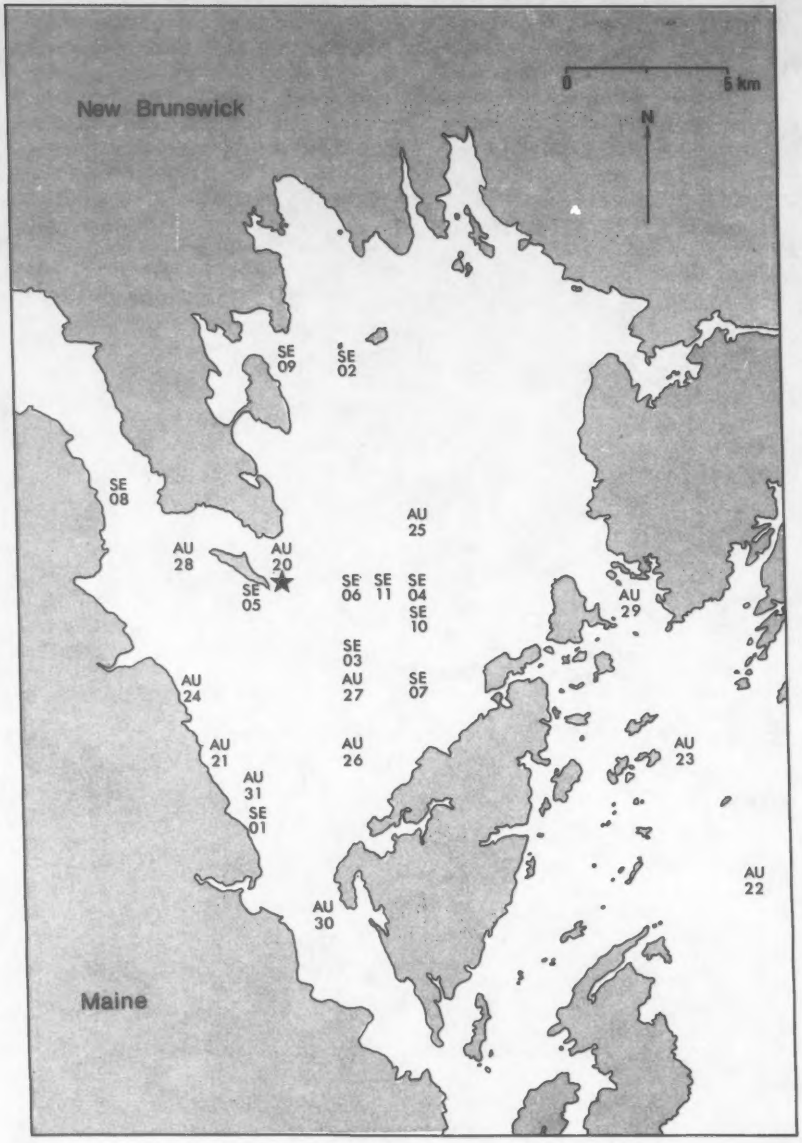

FIGURE 4.—Position of porpoise RT-2 at 1200 of each day of tracking period in the western Bay of Fundy.

The movements of three radio-tagged porpoises (RT-2, RT-4, RT-6) were tracked through the major passages around Deer Island on seven occasions. In all cases, the direction of movement coincided with the direction of tidal flow. The strong correlation between porpoise movements and current direction in these areas was demonstrated on 30 August 1981, when RT-2 moved up Western Passage with the flood tide, turned at slack high water and moved out with the ebb.

Two radio-tagged porpoises were resighted on several occasions. RT-2 was observed resting at the surface in the approaches to Head Harbour Passage on 22 August 1981. Although the porpoise was alone, several groups of resting animals were present in the vicinity. RT-3 was resighted on six occasions; during five of these sightings the radio-tagged animal was accompanied by a single large porpoise. These observations gave no indication that the transmitter packages affected the behavior of tagged porpoises.

Attempts to relocate radio-tagged animals demonstrated some of the inherent problems involved in censusing harbor porpoise populations. Even with the aid of directional receivers and brightly painted transmitters, it was difficult to sight a tagged porpoise or to follow its movements after it had been located. It proved particularly difficult to see radio-tagged porpoises while they lay motionless at the surface.

Patterns of Activity

In total, 39.2 h of ventilation sequences were recorded from four radio-tagged porpoises (RT-2, RT-3, RT-4, RT-7). These sequences comprised 4,680 individual dives, lasting from 2 to 195 s.

Two types of signals were received from radio-tagged animals. The most common signal was brief (1-3 s) and indicated that the porpoise had surfaced and submerged in a continuous motion. Such action patterns are commonly referred to as rolls (Amundin 1974; Smith et al. 1976). Other signals were more prolonged (4-100 s) and are referred to here as surface periods.

Prolonged signals received from radio-tagged harbor porpoises have previously been interpreted as near-surface swimming (Gaskin et al. 1975). However, visual observations of radio-tagged animals RT-2 and RT-3 indicated that such signals originated from porpoises resting motionless at the surface. The strength of the transmitted signal attenuated rapidly as the length of exposed antenna decreased, making it unlikely that signals could be received at any distance from porpoises swimming just below the surface (see also Frost et al.[3]).

Radio-tagged porpoises exhibited two readily discernible activity states (Fig. 5). Low activity (or relative inactivity) was characterized by frequent surface resting periods interspersed with rolls; resting periods accounted for over 55% of all signals in this activity state. Porpoises were considered active (high activity) when resting periods were absent or infrequently recorded. It is important to note that porpoises did not rest at the surface when wave height was >30 cm and winds speeds exceeded 13 km/h (see also Dudok van Heel 1962; Andersen and Dziedzic 1964).

[3]Frost, K. J., L. F. Lowry, and R. R. Nelson. 1983. Investigations of belukha whales in coastal waters of western and northern Alaska, 1982-1983; marking and tracking of whales in Bristol Bay. Final Report, Contract NA 81 RAC 00049, 104 p.

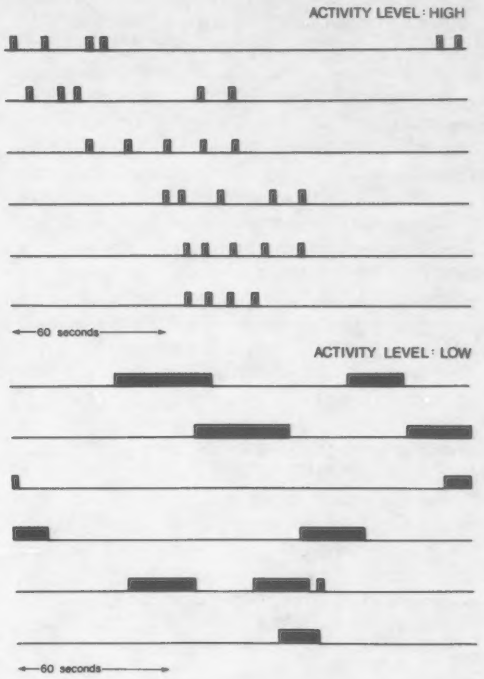

FIGURE 5.—Examples of signal patterns used to derive activity states of radio-tagged harbor porpoises (each example represents a continuous record). Activity level was considered high when signals were dominated by rolls (signal duration 1-3 s). Activity level was considered low when signals were dominated by surface resting intervals (signal duration >3 s). The signal pattern used to demonstrate the high activity level (top) is characteristic of Pattern B respiration (Watson and Gaskin 1983).

Radio-tagged porpoises exhibiting the high activity state expressed two ventilation patterns; these are described using the terminology of Watson and Gaskin (1983). Most data recorded in this activity state consisted of Pattern B, a series of long dives, each followed by a sequence of several rolls (see Figure 5). Less commonly observed was Pattern A, in which single rolls followed relatively short submergences (seldom exceeding 30 s in duration). Pattern A was exhibited for brief periods only (5-16 min) and comprised <4% of all signals recorded during high activity sequences.

Ventilation data recorded from RT-2 and RT-4 were dominated by low activity sequences. However, low activity sequences were not recorded from either RT-3 or RT-7. Although RT-3 was frequently observed resting at the surface, the loose transmitter package (see above) caused the antenna to reflect backwards, allowing signal reception only during rolls. Thus, it was not possible to accurately monitor the duration of resting periods for this porpoise. Data from RT-7 were acquired only during periods of high winds and heavy seas which precluded surface resting behavior.

Because surface resting was the criterion on which determinations of activity levels were based, it was impossible to ascertain the activity level of radio-tagged porpoises in periods of high winds and heavy seas. To construct an activity budget, therefore, it was necessary to exclude data recorded during periods when surface resting was not possible. A total of 10.5 h of ventilation sequences were recorded under such conditions. In addition, data acquired from RT-3 were excluded because of the bias imposed by the transmitting system. After these data had been deleted, 24.5 h of ventilation sequences recorded from RT-2 and RT-4 remained.

Both RT-2 and RT-4 were relatively inactive from midnight until 0600, spending over 90% of this period in the low activity state. Both porpoises spent a considerable portion of this time resting at the surface (Table 2). During this period of reduced activity, the porpoises were seldom located in nearshore areas, although they frequented such areas during other periods. The two porpoises were highly active for 35% (RT-2) and 36% (RT-4) of daylight and evening hours (0600 until midnight) (Table 2).

DISCUSSION

Movements and Ranges

Radio-tagged harbor porpoises demonstrated considerable mobility within the study area, often moving distances of 15-20 km in a 24-h period. These results are similar to those previously reported from radio-tagged harbor porpoises in the region (Gaskin et al. 1975). Other inshore odontocete species exhibit daily movements of a similar magnitude. For example, dusky dolphins, *Lagenorhynchus obscurus*, tracked by Würsig (1982), travelled a "mean minimum distance" of 19.2 km each day. However, pelagic species apparently travel over much greater distances. A pelagic spotted dolphin, *Stenella attenuata*, tracked by Leatherwood and Ljungblad (1979), travelled over 100 km in a 12-h period, while common dolphins, *Delphinus delphis*, may cover distances of 70-140 km each day (Evans 1971).

The mobility exhibited by the majority of radio-tagged porpoises suggest that the ranges of these animals were similar to that calculated for RT-2 (210 km^2). Only one other study has examined the areas of home ranges utilized by odontocete cetaceans. Wells et al. (1980) used resightings of naturally marked animals to estimate the size of bottlenose dolphin, *Tursiops truncatus*, ranges in the coastal waters of western Florida. The mean home ranges of these dolphins varied with age and sex, and ranged from 15 to 41 km^2. It is possible that the apparent difference in the size of home ranges of these two species reflects the exploitation of different prey species. In the Bay of Fundy, harbor porpoises feed predominantly on juvenile herring, *Clupea harengus* (Smith and Gaskin 1974), which exhibit a high degree of mobility (Jovellanos and Gaskin 1983). In contrast, Florida bottlenose dolphins are opportunistic predators on species such as mullet *Mugil cephalus*, which may be more sedentary in nature (Irvine et al. 1981).

Patterns of Activity

The patterns of activity observed in the present

TABLE 2.—Activity patterns of radio-tagged harbor porpoises RT-2 and RT-4 in the western Bay of Fundy. The low activity state was characterized by frequent surface resting periods, which were infrequent or absent in the high activity state. Only data recorded during calm conditions have been included.

Porpoise	Time	Observation time (min)	Activity: high (%)	Activity: low (%)	At surface (%)
RT-2	0000-0559	352.9	2.0	98.0	31.4
	0600-1159	274.8	14.9	85.1	18.8
	1200-1759	435.2	46.0	54.0	11.2
	1800-2359	165.2	41.0	59.0	12.2
Total		1,228.5	25.7	74.3	18.8
RT-4	0000-0559	116.0	7.0	93.0	18.5
	0600-1159	37.0	100.0	0.0	0.0
	1200-1759	0.0	—	—	—
	1800-2359	90.7	9.9	90.1	13.6
Total		243.7	22.2	77.8	13.9

study do not support previous contentions that the metabolic requirements of harbor porpoises (see Kanwisher and Sundnes 1965) are such that individuals must spend a large proportion of each day engaged in foraging behavior (Smith and Gaskin 1974; Watson and Gaskin 1983).

Herbers (1981) has hypothesized that behavioral inactivity is a product of predation efficiency. As predation efficiency increases, less time is spent searching for and capturing prey, and more time is available for other behavior, including inactivity. Therefore, if harbor porpoises are efficient predators, it seems reasonable to suggest that only a small portion of their day would be spent engaged in foraging behavior.

Many other mammalian predators are inactive for large portions of the day. For example, Serengeti lions, *Panthera leo*, are inactive for about 85% of each day (Schaller 1972). Similarly, spotted hyaenas, *Crocuta crocuta*, are inactive for 84% of the day (Kruuk 1972). Even the sea otter, *Enhydra lutris*, with a metabolic rate 2.4 times that predicted for a terrestrial mammal of equal size (Costa and Kooyman 1982), spends only 34% of each day foraging (Loughlin 1979).

The ventilation sequences recorded from RT-2 and RT-4 suggest that these harbor porpoises restricted the majority of their activity to daylight and evening hours (Table 2). If a circadian pattern of activity exists, it may be related to the schooling behavior of prey species. The structure of herring schools breaks down after dusk, as the visual cues used to maintain school structure become inoperative (Brawn 1960). Thus, the fish exhibit a dispersed distribution at night, presumably limiting prey capture by predators such as the harbor porpoises, which rely on dense schools to maintain maximum capture efficiency.

Other odontocete species exhibit various circadian patterns of activity. Observations of captive bottlenose dolphins indicate that, like the harbor porpoise, *Tursiops* is relatively inactive at night (McBride and Hebb 1948; McCormick 1969; Saayman et al. 1973). In contrast, Hawaiian spinner dolphins, *Stenella longirostris*, rest during the day and feed almost exclusively at night (Norris and Dohl 1980). The prey of spinner dolphins undertake extensive vertical migrations (Perrin et al. 1973) and may be more available to the dolphins at night.

We were interested in observing the nocturnal behavior of harbor porpoises (when they were presumably relatively inactive) under conditions of strong winds and heavy seas, when surface resting was not possible. Ventilation data recorded from RT-7 during a 5-h period (0000-0500, 5 September 1982) of heavy seas consisted almost exclusively of Pattern B sequences. Watson and Gaskin (1983) have suggested that this ventilation pattern is expressed primarily by foraging porpoises, but it seems unlikely that RT-7 (a calf) was foraging for 5 consecutive hours at night. An alternative explanation is that the porpoise was resting underwater and rising to the surface for a series of breaths (see similar observations by McBride and Hebb 1948; Layne 1958; McCormick 1969; Condy et al. 1978). It is possible, therefore, that harbor porpoises engaged in diverse behavioral activities may exhibit similar ventilation patterns.

During the period of reduced activity (from 0000 to 0600) radio-tagged porpoises were often located in open water some distance from shore. This may reflect a tendency for porpoises to rest in areas where the hazards of swift currents and shallow waters are minimized. Observations made in the inshore waters of the Deer Island region confirm that porpoises seldom rest at the surface in nearshore environments (Watson and Gaskin 1983).

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LITERATURE CITED

AMUNDIN, M.
1974. Functional analysis of the surfacing behaviour in the harbour porpoise, *Phocoena phocoena* (L.). Z. Saugetierkd. Bd. 39:313-318.

ANDERSEN, S., AND A. DZIEDZIC.
1964. Behaviour patterns of captive harbour porpoise *Phocaena phocaena* L. Bull. Inst. Oceanogr. Monaco 63(1316): 1-20.

ANONYMOUS.
1982. Canadian tide and current tables. Vol. 1. The Atlantic coast and Bay of Fundy. Department of Fisheries and Oceans Canada, Ottawa.

BAILEY, W. B., D. G. MACGREGOR, AND H. B. HACHEY.
1954. Annual variations in temperature and salinity in the Bay of Fundy. J. Fish. Res. Board Can. 11:32-47.

BIGG, M. A.
1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Rep. Int. Whaling Comm. 32:655-666.

BRAWN, V. M.
1960. Seasonal and diurnal vertical distribution of herring (*Clupea harengus* L.) in Passamaquoddy Bay, N.B. J. Fish. Res. Board Can. 17:699-711.

CONDY, P. R., R. J. VAN AARDE, AND M. N. BESTER.
1978. The seasonal occurrence and behaviour of killer whales, *Orcinus orca*, at Marion Island. J. Zool. (Lond.) 184:449-464.

COSTA, D. P., AND G. L. KOOYMAN.
1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. Can. J. Zool. 60:2761-2767.

DORSEY, E. M.
1983. Exclusive adjoining ranges in individually identified minke whales (*Balaenoptera acutorostrata*) in Washington State. Can. J. Zool. 61:174-181.

DUDOK VAN HEEL, W. H.
1962. Sound and Cetacea. Neth. J. Sea Res. 1:407-507.

EVANS, W. E.
1971. Orientation behavior of delphinids: radio telemetric studies. Ann. N.Y. Acad. Sci. 188:142-160.

FORRESTER, W. D.
1960. Current measurements in Passamaquoddy Bay and the Bay of Fundy. J. Fish. Res. Board Can. 17:727-728.

GASKIN, D. E., G. J. D. SMITH, AND A. P. WATSON.
1975. Preliminary study of harbor porpoises (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can. J. Zool. 53:1466-1471.

HERBERS, J. M.
1981. Time resources and laziness in animals. Oecologia 49:252-262.

IRVINE, A. B., M. D. SCOTT, R. S. WELLS, AND J. H. KAUFMANN.
1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fish. Bull., U.S. 79:671-688.

IRVINE, A. B., R. S. WELLS, AND M. D. SCOTT.
1982. An evaluation of techniques for tagging small odontocete cetaceans. Fish. Bull., U.S. 80:135-143.

JOVELLANOS, C. L., AND D. E. GASKIN.
1983. Predicting the movements of juvenile Atlantic herring (*Clupea harengus harengus*) in the SW Bay of Fundy using computer simulation techniques. Can. J. Fish. Aquat. Sci. 40:139-146.

KANWISHER, J., AND G. SUNDNES.
1965. Physiology of a small cetacean. Hvalradets Skr. 48:45-53.

KRUUK, H.
1972. The spotted hyaena. A study of predation and social behaviour. Univ. Chicago Press, Chic., 335 p.

LAYNE, J. N.
1958. Observations on freshwater dolphins in the upper Amazon. J. Mammal. 39:1-22.

LEATHERWOOD, S., AND W. E. EVANS.
1979. Some recent uses and potentials of radiotelemetry in field studies of cetaceans. *In* H. E. Winn and B. L. Olla (editors), Behavior or marine animals, Vol. 3: Cetaceans, p. 1-31. Plenum Press, N.Y.

LEATHERWOOD, S., AND D. K. LJUNGBLAD.
1979. Nighttime swimming and diving behavior of a radio-tagged spotted dolphin, *Stenella attenuata*. Cetology 34, 6 p.

LOUGHLIN, T. R.
1979. Radiotelemetric determination of the 24-hour feeding activities of sea otters, *Enhydra lutris*. *In* C. J. Amlaner and D. W. Macdonald (editors), A handbook on biotelemetry and radio tracking, p. 717-724. Pergamon Press, Oxf.

MACDONALD, D. W., F. G. BALL, AND N. G. HOUGH.
1979. The evaluation of home range size and configuration using radio tracking data. *In* C. J. Amlaner and D. W. Macdonald (editors), A handbook on biotelemetry and radio tracking, p. 405-424. Pergamon Press, Oxf.

MCBRIDE, A. F., AND D. O. HEBB.
1948. Behavior of the captive bottlenose dolphin, *Tursiops truncatus*. J. Comp. Physiol. Psychol. 41:111-123.

MCCORMICK, J. G.
1969. Relationship of sleep, resp iration, and anesthesia in the porpoise: a preliminary report. Proc. Nat. Acad. Sci., U.S. 62:697-703.

NORRIS, K. S., AND T. P. DOHL.
1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish Bull., U.S. 77:821-849.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella*, spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

READ, A. J., AND D. E. GASKIN.
1983. The application of radio tracking techniques to the study of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy. *In* D. G. Pincock (editor), Proceedings of the Fourth International Conference on Wildlife Biotelemetry, p. 346-352. Halifax, Nova Scotia.

SAAYMAN, G. S., C. K. TAYLER, AND D. BOWER.
1973. Diurnal activity cycles in captive and free-ranging bottlenose dolphins (*Tursiops aduncus* Ehrenburg). Behaviour 44:212-233.

SCHALLER, G. B.
1972. The Serengeti lion. A study of predator-prey relations. Univ. Chicago Press, Chic., 480 p.

SMITH, G. J. D., K. W. BROWNE, AND D. E. GASKIN.
1976. Functional myology of the harbour porpoise, *Phocoena phocoena* (L.). Can. J. Zool. 54:716-729.

SMITH, G. J. D., AND D. E. GASKIN.
1974. The diet of harbour porpoises (*Phocoena phocoena* (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Can. J. Zool. 52:777-782.

SMITH, G. J. D., C. L. JOVELLANOS, AND D. E. GASKIN.
1984. Near-surface bio-oceanographic phenomena in the Quoddy region, Bay of Fundy. Can. Tech. Rep. Fish. Aquatic Sci. No. 1280, 124 p.

SMITH, G. J. D., A. J. READ, AND D. E. GASKIN.
1983. Incidental catch of harbor porpoise, *Phocoena phocoena* (L.), in herring weirs in Charlotte County, New Brunswick, Canada. Fish. Bull., U.S. 81:660-662.

SPRINGER, J. T.
1979. Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43:926-935.

WATSON, A. P., AND D. E. GASKIN.
1983. Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* (L.) in coastal waters of the Bay of Fundy. Can. J. Zool. 61:126-132.

WELLS, R. S., A. B. IRVINE, AND M. D. SCOTT.
1980. The social ecology of inshore odontocetes. *In* L. M. Herman (editor), Cetacean behavior: mechanisms and functions, p. 263-317. John Wiley and Sons, N.Y.

WÜRSIG, B.
1982. Radio tracking dusky porpoises in the South Atlantic. *In* Mammals in the seas, Vol. 4, p. 145-160. FAO Fisheries Series No. 5.

EARLY POSTNATAL GROWTH OF THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN THE OFFSORE EASTERN TROPICAL PACIFIC

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ABSTRACT

Estimates of length at birth and early postnatal growth are made for the northern and southern populations of the offshore spotted dolphin in the offshore eastern tropical Pacific. Length at birth is estimated to be 85.4 cm for the northern population and 83.2 cm for the southern population. Analyses of series of monthly distributions of length revealed two cohorts born each year in the northern population, at least in the northern inshore part of its geographic range, but only one cohort born each year in the southern population. Growth curves fitted to the means of the monthly distributions of length gave estimates of length at 1 year of 126.2 and 132.6 cm and length at 2 years of 154.3 and 154.9 cm for the two cohorts in the northern population, and length at 1 year of 127.9 cm for the southern population. A growth curve fitted to lengths and ages (in dental growth layer groups) from the northern population gave estimates of lengths at 1 and 2 years of 123.0 and 143.0 cm, respectively.

The average growth rate of individual animals in a population is an important characteristic because of its correlation with other population parameters. In fisheries biology, two commonly employed techniques used to estimate growth rates are the aging of a sample of fish of known length and the following of a series of length distributions through time. These techniques allow the relationship between length and age (or relative age) to be applied to a much larger sample of fish, provided that the aged sample is a representative one.

For most species of fish, length-age relationships may be appropriate for the entire life of the animals, or at least for the period of interest to a commercial fishery. In marine mammals, however, length changes little, if at all, after attainment of physical maturity. Growth rates may change markedly even while the animal is maturing, being high for an initial period after birth and then declining quite rapidly. In delphinids, the growth rate has been found to be high in the first year, with animals typically increasing by 50-70% of their birth length (Sergeant 1962; Kasuya et al. 1974; Kasuya 1976; Miyazaki 1977; Hohn 1980; Perrin and Henderson 1984), but then declined rapidly in the second year. During this period, growth rates are high relative to the variability in age-at-length so that length distributions are distinguishable as separate age groups. Consequently, length-age relationships for these animals are most useful from birth until about 2 yr.

In this paper, we have used both the technique of following a series of length distributions from month to month and the technique of aging a sample of dolphins of known length to estimate the rate of growth in the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific (hereafter referred to as the offshore spotted dolphin). In neither of these two techniques did we have an absolute measure of age. Consequently, we have estimated length at birth independently and used this to fix time at birth. Growth curves were fitted to the length data by relative age and then length at birth was substituted in order to predict length-at-age.

THE SAMPLE

The field data and specimens used in the following analyses were collected by National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission (IATTC) scientific technicians aboard commercial tuna purse seiners from 1968 to 1982. Procedures for collecting sample data and specimens have been described by Perrin et al. (1976). In all the following analyses, the data have been stratified into northern and southern popula-

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tions divided by lat. 1°S, based on a division selected by Perrin et al. (1979). Areas 1 and 2 in Figure 1 correspond to the region occupied by the southern offshore spotted dolphin and areas 3-8 correspond to the region occupied by the northern offshore spotted dolphin.

ESTIMATION OF LENGTH AT BIRTH

An accurate estimate of length at birth is important because it establishes a point through which any growth curve should pass. This extra degree of freedom allows greater accuracy in fitting growth curves and estimating growth rates. Neither of our methods of relating length to age, described below, allows us to fix absolute age so it is essential here for us to calculate an independent estimate of length at birth.

A commonly used method of estimating length at birth when a sufficient sample is available is to regress the percent postnatal at each length interval on length and to calculate the length at which 50% of the specimens are predicted to be postnatal. This method, using a linear model, has been employed to estimate length at birth for spotted dolphins (Perrin et al. 1976), for striped dolphins, *S. coeruleoalba*, (Miyazaki 1977), and for spinner dolphins, *S. longirostris*, (Perrin et al. 1977), and using a nonlinear model for spinner dolphins (Perrin and Henderson 1984). Another method commonly employed when a small sample is available is to estimate the average length at birth as the mean length of known neonates or the mean length of full-term fetuses and small calves combined. This method has been used to estimate length at birth for long-finned pilot whales (Sergeant 1962), for spotted dolphins (Kasuya et al. 1974), for bottlenose dolphins, *Tursiops truncatus*, (Ross 1977; Hohn 1980), and for

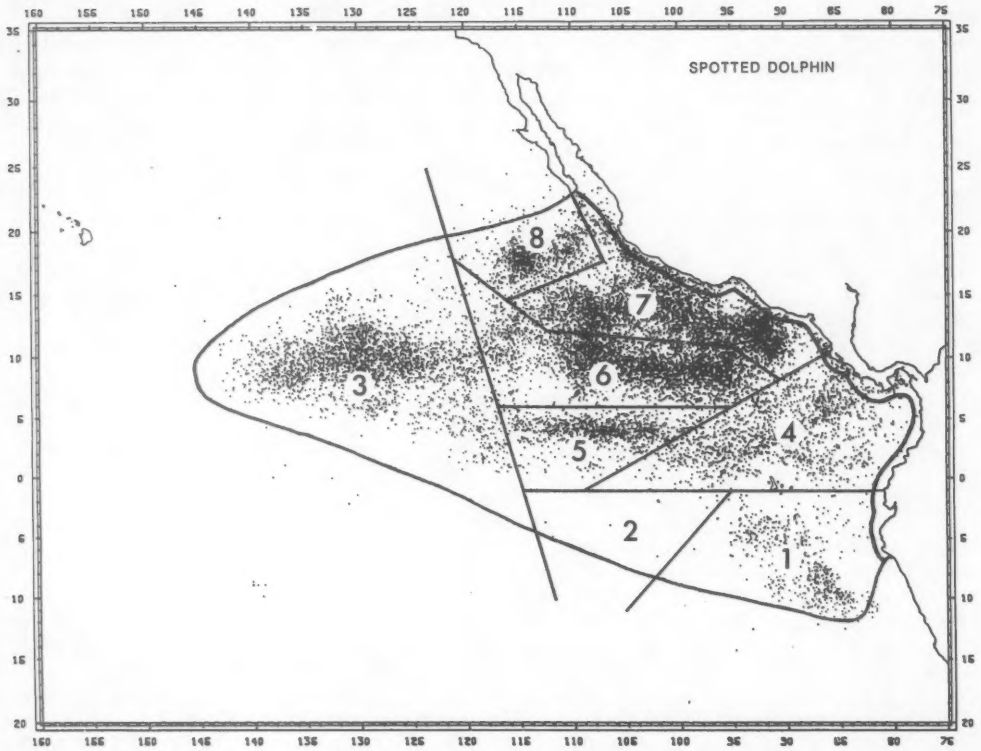

FIGURE 1.—Areas inhabited by the offshore spotted dolphin. The numbered regions refer to strata investigated in analyses of monthly distributions of length. In all analyses, the southern population is from areas 1 and 2, and the northern population is from areas 3 through 8.

the franciscana dolphin, *Pontoporia blainvillei*, (Kasuya and Brownell 1979).

Methods

The data used in this analysis were from all fetuses and calves sampled between 1973 and 1981 except for three specimens <68 cm identified as calves and one specimen of 91 cm identified as a fetus (n = 609). These four specimens were judged to have been misidentified. The data were stratified by area, north and south of lat. 1°S, and the northern sample was further stratified by the size of kill in each net set. Powers and Barlow (1979[3]) have shown that in net sets in which the kill of spotted dolphins from the northern offshore regions was ≤40 (small-kill sets), about twice as many calves were killed as a proportion of the total kill as in sets where the kill was >40 (large-kill sets). This would introduce a bias in the estimate of length at birth in the regression procedure because about 90% of all northern specimens were from small-kill sets. The effect would be to underestimate length at birth because the ratio of calves to fetuses was too high in most of the sample. To investigate the extent of the bias, we calculated average length at birth for all northern specimens, for specimens from sets with kill ≤40 and >40, and for specimens from sets with kill ≤30 and >30 because the sample size for sets with kill >40 was small. The small sample available for southern specimens prevented any further stratification of the data.

Length at birth was estimated by fitting a logistic model to the percent postnatal at each length interval, weighted by the inverse of the binomial variance of each percentage, and estimated by calculating from the fitted curve the length at which 50% of the specimens were predicted to be postnatal. We also investigated linear and asymmetric logistic-type models.

Results

Figure 2 shows the length-frequency data for northern specimens from sets with kill ≤40, and the logistic model fitted to the data. Figure 3 is the equivalent for northern specimens from sets with kill >40. Table 1 gives the results for all stratifications described above using the logistic model. Using the linear or asymmetric logistic-type models did not improve the fit and gave similar results.

Table 1 shows that the estimates of length at birth for northern specimens using the unstratified data (82.0 cm) and using specimens from sets with kill ≤30 (81.6 cm) or ≤40 (81.6 cm) are lower than the estimates using specimens from sets with kill >30 (84.6 cm) or >40 (85.4 cm), demonstrating that the bias resulting from an overrepresentation of calves in small-kill sets is significant. Furthermore, the estimate for kill >40 is higher than that for kill >30, indicated that the proportion of calves in the sample may still be a function of kill-per-set at this level. Further stratification to investigate whether or not estimates of length at birth continue to rise at higher thresholds of kill-per-set was not possible because of small sample size.

The estimate of length at birth for southern specimens is 83.2 cm. No stratification was possible because of the small sample.

Estimates of standard deviations of the estimates of length at birth are not given because, in fitting the logistic model, sums of squares were minimized for differences between observed and predicted percent postnatal and it was unclear how to calculate the standard deviations.

TABLE 1.—Estimates of length at birth stratified by number of offshore spotted dolphins killed per set. The range of length classes includes the last 0% postnatal length class and the first 100% postnatal length class.

	Sample size	Range (cm)	Length at birth predicted from the logistic model (cm)
Northern offshore spotted dolphin			
Unstratified data	586	71-92	82.0
Sets with kill ≤30	321	73-92	81.6
Sets with kill ≤40	384	71-92	81.6
Sets with kill >30	105	71-89	84.6
Sets with kill >40	36	78-89	85.4
Southern offshore spotted dolphin			
Unstratified data	23	78-85	83.2

Discussion

Our estimate of length at birth of 82.0 cm from the unstratified northern data is similar to that of Perrin et al. (1976), who estimated length at birth at 82.5 cm, based on a sample of 73 northern specimens (calves and fetuses) grouped into 3 cm intervals from 74 to 92 cm.

Estimates of length at birth in large-kill sets are less biased because of the overrepresentation of calves in small-kill sets. A future larger sample from large-kill sets may allow for additional stratification by kill-per-set, enabling estimates to be calculated

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, Status of Porpoise Stocks Workshop, La Jolla, CA, 27-31 August 1979. Unpubl. MS.

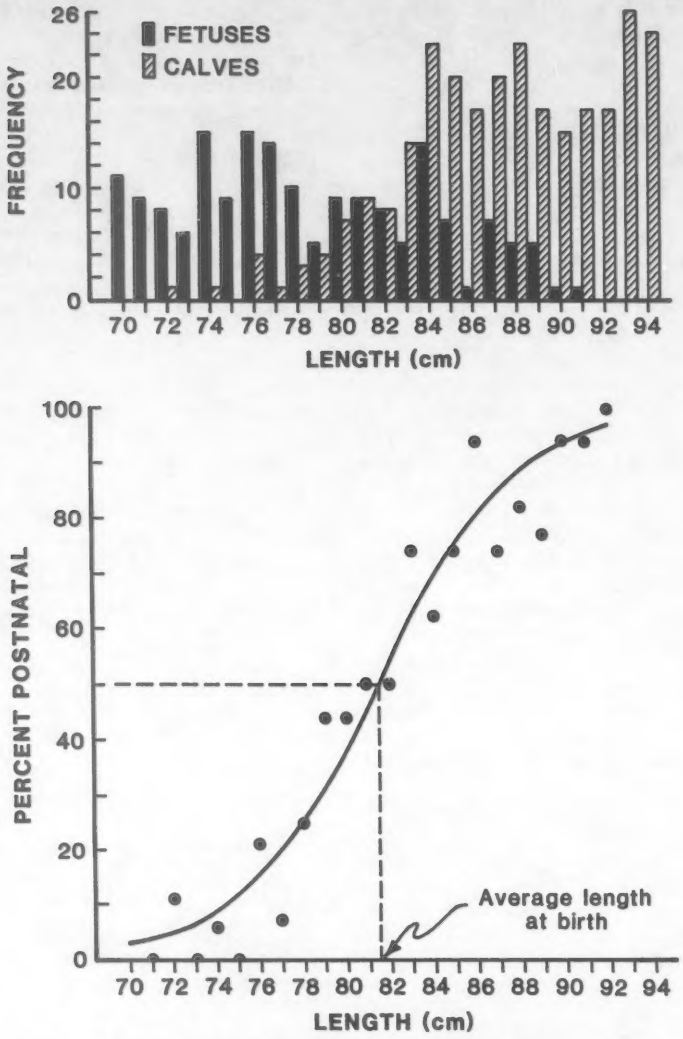

FIGURE 2.—Length-frequency data for specimens from sets with kill ≤40 grouped in 1 cm intervals for 163 fetuses and 221 calves from the northern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

using specimens from sets with higher levels of kill. It may then be possible to determine at what level of kill-per-set the estimate ceases to increase. Until additional data are available, we consider 85.4 cm to be the best estimate of length at birth in northern offshore spotted dolphins.

Our estimate of length at birth in the southern offshore spotted dolphin of 83.2 cm is more questionable because we were unable to stratify by kill-per-set. As adults, southern specimens are about 2.5 cm shorter than their northern counterparts (Perrin et al. 1979). This small, but statistically significant, difference may or may not imply that length at birth is smaller in the southern population. The small sample of 23 specimens used in our calculation of length at birth raises doubts concerning the

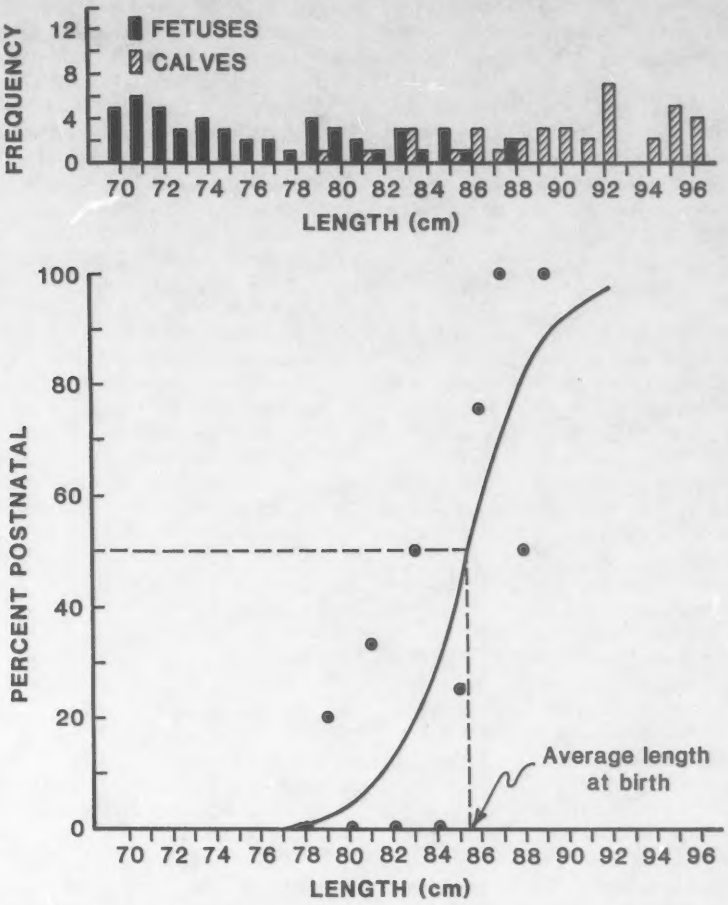

FIGURE 3.—Length-frequency data for specimens from sets with kill >40 grouped in 1 cm intervals for 21 fetuses and 15 calves from the southern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

accuracy of this estimate. For these reasons, we take the estimate from all southern specimens of 83.2 cm as our provisional best estimate of length at birth for southern offshore spotted dolphins while recognizing that this estimate may be biased downwards because of a possible overrepresentation of calves in the sample.

ESTIMATION OF LENGTH-AT-AGE USING ANALYSES OF MONTHLY DISTRIBUTIONS OF LENGTH

Perrin et al. (1976) used the technique of fitting a growth curve to the means of normal distributions fitted to length-frequency data by month to estimate the length of the offshore spotted dolphin at 1 yr of age. Perrin and Henderson (1984) used the same technique for the spinner dolphin. The technique is based on the assumption that breeding in these dolphins is seasonal and that a cohort of animals born at approximately the same time is characterized by a distribution of lengths, identifiable as a mode in the overall length distribution, which can be followed from month to month as mean length of the cohort increases. If there are sufficient data in each month, mean lengths can be followed from birth until

growth slows to an extent that distributions of lengths from different cohorts cannot be distinguished. A growth curve can then be fitted to the monthly mean lengths.

Since the analysis of Perrin et al. (1976), the sample of measured lengths from offshore spotted dolphins has increased from about 3,500 to over 15,000. Consequently, we were able to analyze the available data more extensively than had been done previously.

Methods

Length measurements from all postnatal specimens, made between 1968 and 1982, were used in the analyses except for three specimens <68 cm which were judged to have been erroneously identified as calves. The data were stratified into eight areas based upon apparent hiatuses in distribution from examination of sightings and effort data (Fig. 1). Areas 1 and 2 comprise the southern population and areas 3-8 the northern population.

For the northern data, no consistency could be found in preliminary analyses of lengths when data from all areas were included. When area 3 was excluded, consistency was much improved. When areas 4 and 5 were also excluded, consistency was improved further for the months of February through June. This indicated that there were nonseasonal or seasonal but asynchronous elements in areas 3, 4, and 5 at least at certain times of the year. Consequently, in our analyses of northern data we used lengths from areas 6, 7, and 8 only for February through June and lengths from areas 4-8 for January and July through December. A similar situation occurred for the southern data where the elimination of area 2 improved consistency for January through May. In our analyses of southern data, therefore, we used lengths only from area 1 for these months.

The data were grouped in interval widths of 4 cm. This gave four possible ways of grouping the data because lengths were measured to the nearest whole centimeter. Each of these four groupings were investigated, there being no reason to prefer a starting point of the first interval as, for example, 76, 77, 78, or 79 cm.

A mixture of normal distributions was fitted to each data set using a version of the computer program NORMSEP (Hasselblad 1966). The program requires the number of distributions to be specified, and this was varied in order to determine the most likely number of distributions present. The model selected as most representative of the length-frequency data was that which gave the highest χ^2 value, and therefore the highest probability that a greater χ^2 value could be obtained by chance alone, and also gave biologically feasible results based on prior knowledge of delphinid growth. (Some model fits had a very high probability of a greater χ^2, but the mean lengths could not be accounted for by any reasonable regime of growth.)

We chose Laird's (1969) form of the Gompertz (1825) growth equation to fit to the monthly mean lengths. A linear model is clearly inadequate to describe growth except over a very short time period. We also investigated the use of the von Bertalanffy (1934) growth equation but found it to be less flexible than the Gompertz model.

Each model of growth was fitted to the mean lengths using the midpoint of the first month as time zero. In fact, this is not necessarily the time of birth so we fixed time of birth by substituting our estimate of length at birth into the fitted equation. Lengths at age were then calculated by substituting that age plus the difference between the midpoint of the first month and our calculated time of birth into the fitted equation.

Results

Northern Population

Figure 4 shows, as examples, the fitted mixture of normal distributions to the length-frequency data for August and October. The arrows indicate the positions of the means of the fitted distributions.

Table 2 shows the estimates of mean length of the fitted normal distributions for each month. The estimates are presented so that the increases from month to month can be clearly seen. The two final columns of Table 2 are mean lengths of the two distributions to the right of the length-frequency plots. These mean lengths are consistent from month to month. The table shows that there are actually two series of mean lengths: one beginning at 86.7 cm in September and continuing through columns 2 and 4 of the mean lengths, and the other beginning at 84.5 cm in April (the estimate of 92.7 cm for March is an anomaly for which we have no explanation) and continuing through columns 1, 3, and 5. These represent two cohorts born each year about 6 mo apart in the spring and autumn. Note that each series of mean lengths continues only for about 24 mo. This is because after this time growth has slowed to an extent that it is not possible to distinguish distributions of length from different cohorts. The

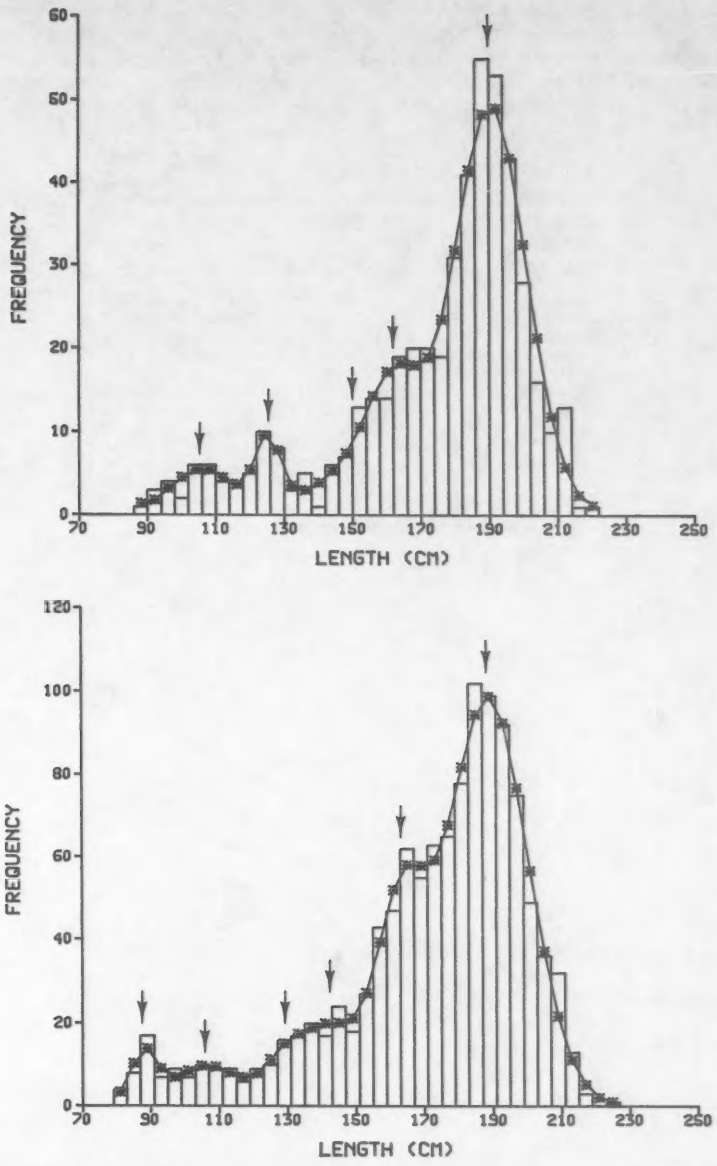

FIGURE 4.—Histograms of length and the fitted mixture of normal distributions for data for the northern offshore spotted dolphin in (A) August and (B) October. The arrows indicate the positions of the means of the fitted distributions.

mean length of 105.9 cm for June was not included in further analyses because its inclusion more than doubled the residual sums of squares for the model fit. We consider it an outlier.

Figure 5 shows Gompertz models of growth fitted separately to the mean lengths, excluding the 92.7 cm point for March, from columns 1, 3, and 5 (curve A) and, excluding the 105.9 cm point for June, from columns 2 and 4 (curve B) of Table 2. Time at birth and lengths at 1 and 2 yr were calculated as

TABLE 2.—Mean lengths of the fitted normal distributions for the northern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)					
September	536		86.7	105.0	129.4	161.3	186.9
October	1,159		87.9	106.3	129.4	142.7	163.1	188.8
November	616		91.9	113.9	129.6	145.7	159.4	187.7
December	223		97.5		127.7	149.9		187.4
January	2,926		102.9		142.4		161.9	187.4
February	2,772		104.1		140.7	151.8	161.5	186.3
March	866	[1]92.7	113.2	131.4			160.7	188.7
April	700	84.5	113.6		146.0		163.6	188.5
May	423	84.5	108.7	133.9	147.5		165.9	187.9
June	300	90.7	[1]105.9	135.5			165.2	189.5
July	266	91.8	118.0	136.1	150.8		164.5	190.1
August	486	105.7	125.1		151.8		162.6	190.5

[1]These mean lengths were not included in further analyses.

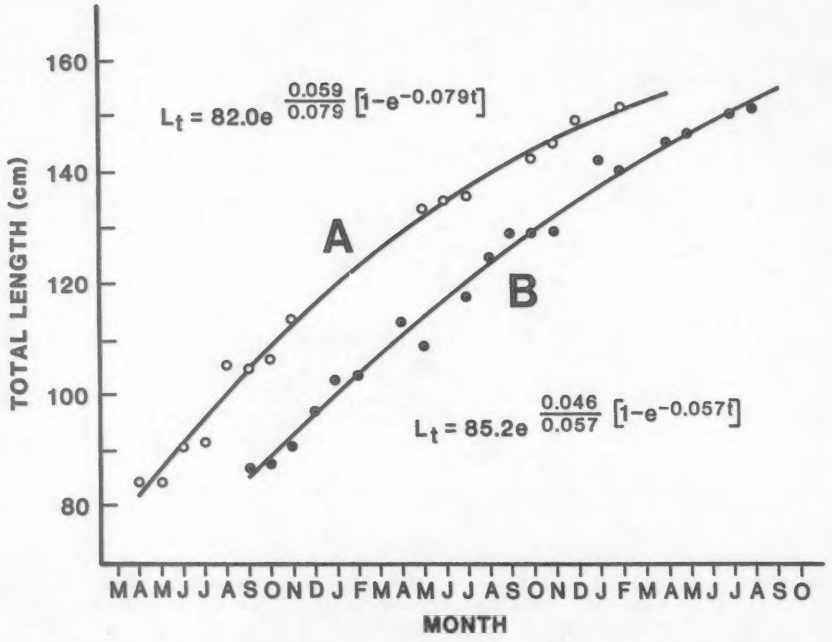

FIGURE 5.—Mean values of monthly distributions of length from data for the northern offshore spotted dolphin. The two curves represent two annual cohorts fitted separately by the Gompertz model of growth. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

described above with the following results:

	Growth curve A	*Growth curve B*
Fixed length at birth (estimated in this paper)	85.4 cm	85.4 cm
Estimated time of birth	May 9	September 11
Estimated length at 1 yr	132.6 cm	126.2 cm
Estimated length at 2 yr	154.9 cm	154.3 cm

Rates of growth as centimeters per month for the two fitted curves adjusted for length at birth are as follows:

	Rate of growth	
Months after birth	*Curve A*	*Curve B*
0	5.03	3.80
6	3.94	3.43
12	2.76	2.89
18	1.81	2.33
24	1.14	1.82

Southern Population

Table 3 shows the estimates of mean length of the fitted normal distributions for each month. For these data it is clear, apart from the mean lengths of 105.0 cm in January and 127.5 cm in May, that there is only one cohort born each year in the southern summer. As a result of this and the much smaller sample sizes, distributions of length could only be distinguished up to about 18 mo. The two final columns of Table 3 show the mean lengths of the two distributions to the right of the length-frequency plots. These are quite consistent from month to month, as with the northern data.

Figure 6 shows the Gompertz model of growth fitted to the mean lengths from columns 1 and 3 of Table 3. Time at birth and length at 1 yr were calculated as described above with the following results:

Fixed length at birth (estimated in this paper)	83.2 cm
Estimated time of birth	6 January
Estimated length at 1 yr	127.9 cm

Rates of growth for this fitted curve do not decrease from birth as they do for the northern population because the curve has a point of inflection at approximately 50 mo. The rates of growth at 0, 6, 12, and 18 mo after birth are 3.29, 3.72, 4.12, and 4.47 cm/mo, respectively.

TABLE 3.—Mean lengths of the fitted normal distributions for the southern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)				
December	47	81.0		123.5	165.7	187.9
January	254	87.0	[1]105.0	131.0	164.5	187.8
February	412	85.1		134.9	165.6	188.0
March	57	90.0		139.3		189.7
April	43	97.9		140.8	163.3	189.5
May	212	97.1	[1]127.5	144.3	157.7	182.6
June	42	99.0			163.8	185.3

[1]These mean lengths were not included in further analyses.

Discussion

There are several sources of variability in the estimates of mean length by month to which the growth models have been fitted. There is individual variation in time of birth, length at birth, and growth rate. The calving season may vary from year to year and area to area. The specimens which were measured are subject to the usual sampling variation. Sampling in a particular year may not have been random with respect to time in each month. Given these sources of variability, it is interesting that the results should appear so consistent.

The growth curves were fitted to the unweighted mean lengths. If the variation in the mean length of a distribution is considered to be due largely to sampling error, then there is a justification for a weighted regression. We believe that this is not necessarily the case and that the unweighted regressions represent the best descriptions of growth for these data. When weighted regressions were performed the fitted curves changed negligibly.

The most important potential problem is that the method relies upon being able to analyze a sample of data in which reproduction is seasonal and in which the timing of seasonality is constant. This analysis has shown that this may be difficult to achieve. Only by stratification of the data by area could consistent results be obtained. Stratification of the data by area improves the consistency of the series of mean lengths because offshore spotted dolphins appear to have different calving seasons depending upon the area of capture. In probability, this seasonality is not actually a function of area but of schools or groups of schools which tend to inhabit different areas with different environmental conditions. Thus, even with the best stratification scheme, there may always be asynchronous seasonal elements in a sample of data from any given area affecting the estimation of the mean lengths of the cohorts.

In this analysis we pooled the data from several years for our monthly samples, rather than attempt-

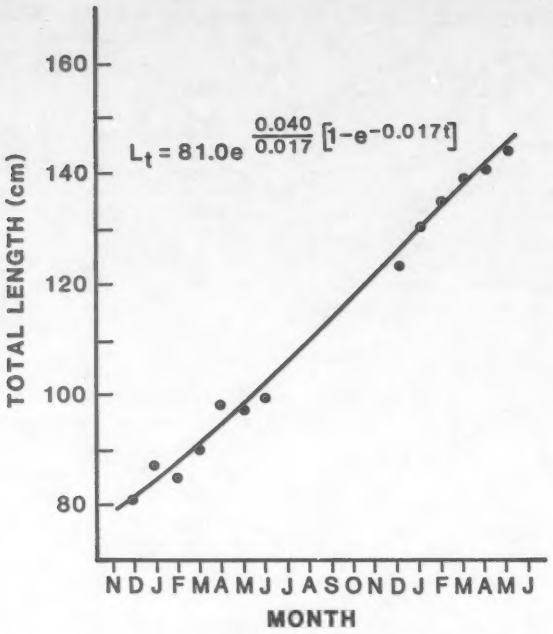

FIGURE 6.—Mean values of monthly distributions of length from data for the southern offshore spotted dolphin. The curve represents one annual cohort fitted by the Gompertz model of growth. The open circles were not included in the fitting of the curve. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

ing to follow actual cohorts of animals from individual years as did Perrin et al. (1976) in their analyses. Combining the data from several years introduces additional variation in the data if the timing of the calving season varies from year to year, but it increases sample sizes and minimizes bias caused by nonrandom timing of sampling within months. In addition, we are mainly interested in an average growth rate which is best estimated from several years of data.

Perrin et al. (1976) fitted a linear model to mean lengths estimated in the months of October 1972, January, February, March, and April through June 1973 from which they extrapolated to obtain an estimate of length at 1 yr of 147.5 cm for the northern offshore spotted dolphin. The authors recognized that this estimate was biased upwards because growth rates of delphinids do decrease in the first year and revised this estimate downwards based on aged specimens. We believe our analyses to be more accurate than those of Perrin et al. (1976) and our results to be a substantial improvement.

Barlow (1984) found an indication of two peak calving seasons for spotted dolphins north of the Equator, in the spring and autumn, but that the animals were born throughout the year. South of the Equator he found a single season peaking around April. These results are similar to ours but the timing of the southern season does not agree. The difference can be explained by Barlow's use of Perrin et al.'s (1976) growth curve which predicted a mean length of 138.0 cm for 1-yr-old animals. Our growth equations predict animals of this length to be from 14 to 16 mo old.

The two growth curves fitted to the mean lengths from the two cohorts in the northern region predict different lengths-at-age and are characterized by very different growth rates. It is possible that these two cohorts actually grow at different rates because of environmental factors, but we believe that the dif-

ferences are more likely a result of variability in the data. We suggest, therefore, that the mean of the estimates from both growth curves be used for estimates of lengths-at-age for the northern offshore spotted dolphin.

For the southern population, the mean lengths of 105.0 and 127.5 cm for January and May, respectively, suggest that there may be two calving seasons in this area. At present, the sample size is too small to assess whether or not this is the case.

ESTIMATION OF LENGTH-AT-AGE USING GROWTH-LAYER-GROUP (GLG) AGING

Increments of tissue are deposited in teeth as a function of time. The most important incremental pattern in odontocete teeth is comprised of growth layer groups (GLGs), defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine, cementum, or bone which is defined as a countable unit" (Perrin and Myrick 1980, p. 48-49). These GLGs are used for age determination in many species of odontocetes, as well as pinnipeds and sirenians (see review by Scheffer and Myrick 1980), but in most species no calibration of GLGs with absolute time is available. However, a few known-age captive and minimum-known-age captive bottlenose dolphins (Sergeant 1959; Sergeant et al. 1973; Hui 1978) and captive tetracycline-marked specimens of other species (*Lagenorhynchus obscurus*, Best 1976; *Delphinus delphis*, Gurevich et al. 1980; *S. longirostris*, Myrick et al. 1984) have provided evidence that the GLG as defined and calibrated by these workers represents an annual deposition pattern. In the absence of any known-age specimens of spotted dolphins, we have assumed that a GLG pattern similar to that described in the above species represents the same amount of time.

Methods

A sample of 800 males and 800 females, selected randomly from the specimens collected between 1973 and 1978, and all 312 female specimens collected in 1981 made up the sample of animals from which teeth were aged.

The teeth were decalcified in RDO[4], a commercial decalcifying agent, cut longitudinally into 24 μm thin sections using a freezing microtome, stained in haematoxylin, and mounted in 100% glycerin. Detailed procedures for the preparation technique and interpretation of GLGs are described by Myrick et al. (1983).

Teeth from each of the 1,600 specimens collected between 1973 and 1978 were "read" for age at least three times, to the nearest 0.1 GLG in young animals, by each of two readers over a period of 2 yr. The series of age estimates was averaged for each reader, and the resulting two mean age estimates were again averaged to produce a pooled mean age estimate (see Reilly et al. 1983). Only one age reading was made by each reader for the 312 specimens collected in 1981, and the mean of these two readings determined. For lack of a preference for one reader's estimates, growth rate analyses used the pooled mean and mean age estimates. Growth models were fit to the age-length data for males and females separately.

Growth rate was estimated by regressing length on number of GLGs (age) using Laird's (1969) form of the Gompertz model. The data were truncated at ≤3.0 GLGs in order to reduce the effects of older animals on our estimates of growth in the first 2 yr, in case the chosen model failed to describe growth adequately over a wider range of ages. Length at birth was fixed at the independently estimated value of 85.4 cm (see above).

Results

There was no difference in growth between males and females at this age. Therefore, the data were pooled. Figure 7 shows the Gompertz model of growth fitted to the pooled data. The model gives a predicted length of 123 cm (SD = 0.7 cm) at 1 yr and a predicted length of 143 cm (SD = 0.6 cm) at 2 yr. These standard deviations are underestimates because they do not incorporate variability in the age of individual specimens resulting from between reader differences.

Figure 7 also shows that lengths predicted by this model may be underestimated up to about 8 mo and overestimated from about 8 to 13 mo. For comparison with predicted length at 1 yr from the model, the mean length of specimens aged between 0.9 and 1.1 yr (n = 24) is 121 cm with a range of 101-140 cm.

The estimated monthly growth rate is 3.84 cm/mo initially, falling to 3.11 cm/mo at 6 mo, 2.33 cm/mo at 12 mo, 1.67 cm/mo at 18 mo, and 1.15 cm/mo at 24 mo.

Discussion

The accuracy of these length-at-age estimates

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

depends upon the representativeness of the sample, the accuracy of the readings, the assumptions that 1 GLG equals 1 yr, and the adequacy of the growth model.

The sample analyzed was a simple random sample, stratified only by sex, taken from all specimens collected between 1973 and 1978. These were themselves a sample of the animals killed incidental to fishing operations, which were a sample of the population. Although Powers and Barlow (fn. 2) have shown a bias towards a higher proportion of calves killed in purse seine nets, we have no reason to believe that the relationship between length and age is different in our sample than in the population.

Teeth were read as accurately as possible. Reilly et al. (1983) have investigated the precision of the readings but, without known-age animals, it is not possible to validate their accuracy.

Our assumption that 1 GLG equals 1 yr is based on captive, tetracycline-marked Hawaiian spinner dolphins (Myrick et al. 1984) a distantly related species. Known-age, captive or marked spotted dolphins are not available for direct GLG calibration. If differences are found between GLG in spotted and spinner dolphin teeth when data from known-age spotted dolphins are available, these estimates of growth based on GLGs will need to be revised.

It is often assumed that when one GLG is deposited each year the first GLG begins with the neonatal line immediately at birth and ends precisely 1 yr later. Yet it is possible, as suggested by Perrin et al. (1977) for *S. longirostris*, that the first GLG is not always complete. Teeth from young, known-age dolphins from the same stock born at different times during the year are needed to address this question.

It is also possible that the neonatal line may not be deposited immediately at the time of birth. In bottlenose dolphins, stranded on the mid-Atlantic coast of the United States, variability has been found in the time of deposition of the neonatal line in 18 neonatal specimens (Hohn unpubl. data). These specimens were identified as neonates because they lacked the umbilicus (indicating that the calf was not stillborn) and their dorsal fin and flukes were folded (Tavolga and Essapian 1957). Some of these stranded specimens showed no neonatal line while others had part of a neonatal line deposited. Similarly, in our sample of offshore spotted dolphins from northern areas there is not neonatal line in some postnatal specimens so that the amount of time since birth is unknown. This difference in timing of neonatal line deposition may be due to individual variation in tooth growth and mineralization or small difference in gestation time.

The precise timing of the deposition of the first

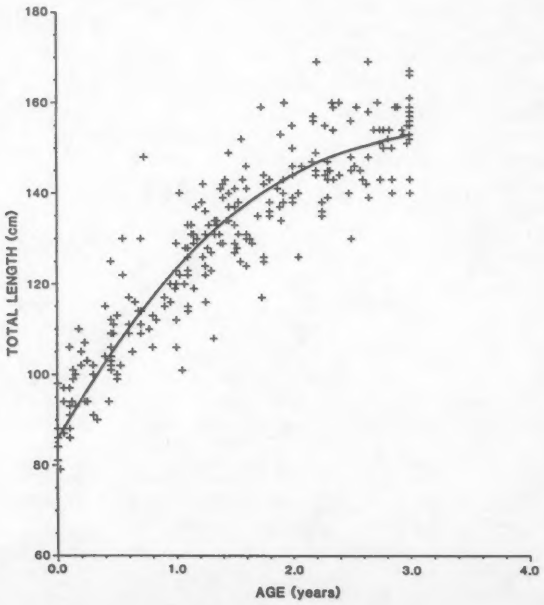

FIGURE 7.—Length-age [GLGs, (growth layer groups), pooled mean estimates] data for northern offshore spotted dolphins up to 3.0 GLGs, and the fitted Gompertz model of growth.

GLG (beginning with the neonatal line) is important in estimates of age in young animals. For a specimen estimated to be 0-yr-old based on GLGs but which is known not to be a neonate, the age must necessarily be an underestimate of the actual age of that specimen, and, consequently, the average length of "0-yr-olds" would be greater than the average length of new-born specimens. When the Gompertz model (with L_0 not fixed) is fitted to the age data, the predicted length at age 0 is 89.6 cm, 4.2 cm higher than the length-at-birth estimate. The age at which the predicted length is 89.6 cm when L_0 is fixed at 85.4 cm is about 0.1 GLGs. This indicates a possible bias of about 0.1 GLGs for young animals. However, this difference between predicted length for fits of the model with fixed and floated L_0 diminishes rapidly and at 0.7 GLGs predicted length is 114.0 cm for both models.

The Gompertz model appears to be generally suitable in describing the early growth of the offshore spotted dolphin based on GLG readings. However, the pattern of points around the fitted line in Figure 7 up to about 1.1 GLGs indicates that growth during this period may not be adequately described by a single curve. This pattern may be a result of either sampling variation or errors in reading, but it may be due to changes in growth rate during this period resulting from changes in food intake. Perrin et al. (1976) have estimated that weaning occurs at about 11 mo in the offshore spotted dolphin so that during the period from about 8 to 13 mo, milk intake will be decreasing and the intake of solid food will be increasing. Growth rates may well reflect these changes. If this is the case, a two-cycle model may describe growth more accurately during this period. Such an approach was used by Perrin et al. (1976, 1977) in spotted and spinner dolphins, respectively, to describe a secondary surge in the growth of pre-adult animals.

CONCLUDING REMARKS

Our analyses have produced different estimates of growth rates and lengths-at-age from two different techniques. The reliability of fitting growth curves to series of means of identifiable distributions of length by month depends primarily upon being able to select a sample in which breeding is both seasonal and synchronous from year to year. The reliability of fitting growth curves to length-age data as determined by counting GLGs depends primarily upon the validity of the assumption that 1 GLG is equivalent to 1 yr. We believe that neither technique is sufficiently reliable to be labelled as the "best" method or to try to calibrate the other. Rather, our analyses underline the need for the analysis of data collected from known-age animals of these populations. However, we do believe that the estimates of growth rates and lengths-at-age presented here are the best currently available for offshore spotted dolphins from the eastern tropical Pacific.

ACKNOWLEDGMENTS

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LITERATURE CITED

BARLOW, J.
1984. Reproductive seasonality in pelagic dolphins, (*Stenella* spp.): Implications for measuring rates. *In* W. F. Perrin, D. P. DeMaster, and R. L. Brownell (editors), Reproduction in cetaceans, p. 191-198. Rep. Int. Whaling Comm. Spec. Issue 6.

BEST, P. B.
1976. Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin, *Lagenorhynchus obscurus*. S. Afr. J. Sci. 72:216-218.

GOMPERTZ, B.
1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of Life Contingencies. Philos. Trans. R. Soc. Lond. 115:513-585.

GUREVICH, V. S., B. S. STEWART, AND L. H. CORNELL.
1980. [1981]. The use of tetracycline in age determination of common dolphins, *Delphinus delphis*. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 165-170. Rep. Int. Whaling Comm. Spec. Issue 3.

HASSELBLAD, V.
1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

HOHN, A. A.
1980. Age determination and age related factors in the teeth of western North Atlantic bottlenose dolphins. Sci. Rep. Whales Res. Inst., Tokyo 32:39-66.

HUI, C.
1978. Reliability of using dentine layers for age determination in *Tursiops truncatus*. U.S. Dep. Commer., Natl. Tech. Inf. Serv., PB288444, 25 p.

KASUYA, T.
1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Sci. Rep. Whales Res. Inst., Tokyo 28:73-106.
KASUYA, T., AND R. L. BROWNELL, JR.
1979. Age determination, reproduction, and growth of Franciscana dolphin *Pontoporia blainvillei*. Sci. Rep. Whales Res. Inst., Tokyo 31:45-67.
KASUYA, T., N, MIYAZAKI, AND W. H. DAWBIN.
1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst., Tokyo 26:157-226.
LAIRD, A. K.
1969. The dynamics of growth. Res. Dev. 20(8):28-31.
MIYAZAKI, N.
1977. Growth and reproduction of *Stenella coeruleoalba* off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst., Tokyo 29:21-48.
MYRICK, A. C., JR., E. W. SHALLENBERGER, I. KANG, AND D. B. MACKAY.
1984. Calibration of dental layers in seven captive Hawaiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. Fish. Bull., U.S. 82:207-225.
MYRICK, A. C., JR., A. A. HOHN, P. A. SLOAN, M. KIMURA, AND D. STANLEY.
1983. Estimating age of spotted and spinner dolphins, (*Stenella attenuata* and *Stenella longirostris*) from teeth. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-30, 17 p.
PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.
PERRIN, W. F., AND J. R. HENDERSON.
1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *In* W. F. Perrin, D. P. DeMaster, and R. L. Brownell (editors), Reproduction in cetaceans, p. 417-430. Rep. Int. Whaling Comm. Spec. Issue 6.
PERRIN, W. F., D. B. HOLTS, AND R. B. MILLER.
1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.
Perrin, W. F., and A. C. Myrick, Jr. (editors).
1980. [1981]. Age determination of toothed whales and sirenians. Rep. Int. Whaling Comm. Spec. Issue 3, 229 p.
PERRIN, W. F., P. A. SLOAN, AND J. R. HENDERSON.
1979. Taxonomic status of the 'south-western stocks' of spinner dolphin *Stenella longirostris* and spotted dolphins *S. attenuata*. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 175-184. Rep. Int. Whaling Comm. 29.
REILLY, S. B., A. A. HOHN, AND A. C. MYRICK, JR.
1983. Precision of growth layer group ageing of spotted dolphins. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-35, 27 p.
ROSS, G. J. B.
1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. Ann. Cape Prov. Mus. (Nat. Hist.) 11:135-194.
SCHEFFER, V. B., AND A. C. MYRICK, JR.
1980. [1981]. A review of studies to 1970 of growth layers in the teeth of marine mammals. *In* W. F. Perrin and A. C. Myrick, Jr. (editors), Age determination of toothed whales and sirenians, p. 51-64. Rep. Int. Whaling Comm. Spec. Issue 3.
SERGEANT, D. E.
1959. Age determination of odontocete whales from dentinal growth layers. Norsk Hvalfangst-Tid. 48:273-288.
1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Fish. Res. Board Can., Bull. 132, 84 p.
SERGEANT, D. E., D. K. CALDWELL, AND M. C. CALDWELL.
1973. Age, growth, and maturity of bottlenose dolphin (*Tursiops truncatus*) from northeast Florida. J. Fish. Res. Board Can. 30:1009-1011.
TAVOLGA, M. C., AND F. S. ESSAPIAN.
1957. The behavior of the bottle-nosed dolphin (*Tusiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zoologica (N.Y.) 42(1):11-31.
VON BERTALANFFY, L.
1934. Untersuchungen über die Gesetzlickeit des Wachstums. Wilhelm Roux' Arch. Entwichlungsmech. Org. 131:613.

FACTORS AFFECTING THE GROWTH OF UNDERSIZE WESTERN ROCK LOBSTER, *PANULIRUS CYGNUS* GEORGE, RETURNED BY FISHERMEN TO THE SEA

R. S. Brown and N. Caputi[1]

ABSTRACT

The Western Australian fishery for the western rock lobster, *Panulirus cygnus*, yielded about 12,400 t, valued at $A100 million, in 1982-83. It is the largest single species fishery in Australia and one of the largest rock lobster fisheries in the world.

During a season, between 16 and 20 million undersize rock lobsters are brought aboard the vessels by normal fishing operations, despite the escape gaps in all professional and amateur pots. All undersize animals must be returned by fishermen to the sea, but to accomplish this it took from a few minutes to hours, depending on the sorting technique used. The negative effects of handling on the survival of the undersize lobsters have been previously reported, but another important aspect is the effect of handling (damage, exposure, and displacement) on the growth rate of returned undersize rock lobsters.

Two laboratory experiments showed that growth increment at the first molt after air exposure was significantly reduced, and in one of the experiments it was also significantly reduced for the second molt after exposure.

Three field tagging trials were conducted with 6,700 undersize rock lobsters. One trial showed that exposure had a significant detrimental effect; the other trial in which exposure was tested, there was a negative, but not significant, trend. Damage (number of appendages lost) and displacement from the home range significantly reduced the growth increment in each of the three tagging trials. The growth increment of damaged animals was inversely proportional to the number of appendages lost by the animal with sizes ranging from 0.33 to 0.48 mm smaller per appendage missing. The losses to the fishery and other associated problems caused by the reduced growth of the undersize lobsters are discussed.

The fully exploited stocks of western rock lobster, *Panulirus cygnus* George, support the largest single species fishery in Australia and one of the largest rock lobster fisheries in the world, averaging 10,000 t for the last 9 yr to 1982-83. In 1982-83 the fishery recorded its best season; the 12,400 t worth about $A100 million, were landed by 780 boats licensed to participate in the industry. The amateur catch from the fishery, estimated at 1.6% of the professional catch (Norton 1981), is considered to be a relatively insignificant component of the total fishery, though it may be locally important and occurs in shallow areas where large numbers of undersize rock lobsters (i.e., those with a carapace length <76 mm and referred to below as undersize) are caught.

Fishing pressure on the rock lobster stock has been increasing steadily during the past 20 yr, even though it has been a limited entry fishery since 1963 (Morgan 1980a, b; Hancock 1981). This has led to the need for constant monitoring of the fishery and the updating of management procedures and regulations to ensure the stability and viability of the rock lobster stock (Bowen 1980; Morgan 1980a, b; Hancock 1981; Morgan et al. 1982). An important component of management of a fully exploited stock is to reduce waste, e.g., by predation and poor handling techniques.

Two of the most important regulations that aid in conservation of the western rock lobster stock pertain to undersize:

1) Compulsory use of a 54 × 305 mm escape gap in each of the 76,000 professional and all amateur pots (traps) in the fishery allows many undersize animals to escape before the pot is pulled (Bowen 1963).
2) Undersize lobsters that do not escape and are brought aboard must be returned to the sea.

Although use of escape gaps reduces the retention of undersize lobsters by over 50% (Bowen 1963; Brown unpubl. data), between 16 and 20 million undersize animals are still handled each season by professional fishermen (Brown and Caputi 1983). The latter authors found that the handling practices of fishermen, which cause exposure, damage

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(number of legs and antennae missing), and displacement of undersize lobsters, resulted in a drop in recapture (mainly due to mortality) of 14.6%. After allowing for the natural mortality expected before the undersize lobsters would reach legal size, the effective reduction that could be expected was 11.4%. For the 1982-83 season, the loss to the fishery could have been in the vicinity of $A8 million.

An aspect of undersize lobster mortality and loss of commercial production that was not discussed by Brown and Caputi (1983) concerns the effect of handling on the growth of these animals. If the growth rate of the undersize lobster is reduced by exposure, damage, and displacement, then it could affect the rock lobster stock and the commercial fishery in a number of important ways as discussed by Davis (1981): 1) The time taken for undersize lobsters to reach legal size would be increased; 2) these animals would enter the commercial fishery at a smaller size than those with unhindered growth; and 3) the size at which these animals would attain maturity would be reduced.

Other researchers have shown that the growth rate of crustaceans generally and rock lobsters in particular is affected by a variety of environmental factors such as food availability, temperature, photoperiod, molt phase, injuries, shelter availability, salinity, and others (Chittleborough 1974a, 1975, 1976; Aiken 1980). Far less information is available on the effects of commercial and recreational fishing practice on the growth rates of exploited rock lobster or other crustacean populations (Davis and Dodrill 1980; Davis 1981). Information that is available deals almost exclusively with the injury (damage) component of fishing activities or experimentation. Injury, recorded as the loss of appendages, has been shown to affect significantly the growth of rock lobsters *P. cygnus* (Chittleborough 1975) and *P. argus* (Davis 1981) and the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* (Kuris and Mager 1975).

This paper reports effects of three major components of the capture and release experience (i.e., damage, exposure, and displacement) on the growth rate of undersize lobsters caught from commercially fished populations of *P. cygnus*. The effect of the various components was examined by tagging lobsters that were exposed for various periods and were displaced at different distances from their place of capture, with any damage being recorded. Growth of experimental animals between release and subsequent recapture was compared with that of control lobsters which had not been exposed, damaged, or displaced. Laboratory experiments were also conducted in which undersize lobsters were exposed for various periods and their growth rates subsequently monitored over the next two molts.

Consequences to the industry of any reduction in growth rate are discussed in the light of results from this research and the findings reported by Brown and Caputi (1983).

LABORATORY EXPERIMENTS

Materials and Methods

Exposed undersize lobsters were maintained under otherwise near optimal growing conditions of excess food, adequate shelter, and protection from potential predators (see also Chittleborough 1975) and their molt increment and intermolt period compared with those of unexposed animals.

Undersize lobsters (72-75 mm carapace length) were collected from the field and transported in aerated seawater tanks to the laboratory in January 1978. Each animal was examined for size, sex, and damage. Sixty undersize lobsters with no damage or maximum of one appendage missing were selected and marked with numbered squares of Dymo Scotch Tape,[2] fixed to the dorsal side of the carapace with Repco Super Glue and placed in open circulation seawater tanks. Aquaria were checked daily for molts, and animals were fed to excess on whole live mussels and fresh fish. If molting had occurred, the exuvia was removed and the newly molted animal left for a week to harden before measuring and renumbering. In January 1979, each animal was allowed to undergo a minimum of two molts before the entire group (Group I, consisting of 4 subgroups of 15 animals) was given exposures of 0, 15, 30, or 60 min at a temperature of 34°35°C. Animals that died prior to exposure were not replaced.

After exposure, undersize lobsters were returned to their tanks and were checked daily for any molts or deaths. Feeding and renumbering was continued as for pre-exposure. Every animal that survived was allowed at least two molts before the experiment was terminated.

A second group of undersize lobsters (Group II, consisting of 5 groups of 12 animals), collected in June 1978, were treated in the exact manner as described for Group I with the exception that exposures of 0, 15, 30, 60, or 120 min at 20°21°C took place 18 mo later, in December 1979.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

In the January 1979 exposure experiment (Group I), all eight undersize animals exposed for 60 min died before the second molt after exposure, while one animal died from each of 0-, 15-, and 30-min exposure categories leaving 7, 10, and 7 animals respectively.

An analysis of variance on growth increment at the first molt after exposure showed that exposure was significant ($P < 0.01$) after other factors (e.g., sex, damage, initial size), which may have affected growth, were taken into account. However, at the second molt after exposure, the effect of exposure on growth increment was not significant ($P > 0.05$). An analysis of variance on the time taken (days) between the last molt before exposure and first molt after exposure (intermolt period) resulted in exposure being not significant. Exposure was also not significant for the following intermolt period.

In the December 1979 exposure experiment (Group II), one animal died in the 0-, 15-, 30-, and 120-min exposure categories and two died from the 60-min exposure before the second molt after exposure. In this experiment, exposure had a significant effect on the growth increment for both the first ($P < 0.001$) and the second ($P < 0.01$) molts after exposure. An analysis on the intermolt period for the first molt after exposure showed no significant effect due to exposure, but exposure was significant ($P < 0.05$) for the following intermolt period, mainly due to the low number of days between molts for animals in the 120-min exposure category.

TAGGING TRIALS

Materials and Methods

There are two main events in the commercial fishery for *P. cygnus* which follow molting by a large proportion of the population. The first event is in November-December when maturing 4-5 yr old pale-shelled animals known locally as "whites" move offshore into deeper water, where the breeding stock is generally situated. During the "whites" fishery, about 40% of the total catch is taken (Morgan 1980b). The second event is in March-April when postmolt, dark-shelled, sedentary animals called "reds" are captured (George 1958; Morgan 1977). As already mentioned in Brown and Caputi (1983), account had to be taken of these two periods when planning tagging trials as the migratory "whites" could be more mobile and in a physiologically different state than nonmigratory "reds" and hence their growth could be affected differently by handling practices (i.e., causing exposure, displacement, and damage). With these possible differences in mind, three tagging trials were conducted at Two Rocks, Western Australia (lat. 31°29.7′S, long. 115°31′E), avoiding the period of the full moon, when catches are at their lowest (Morgan 1974, 1977): 1) migratory "whites" phase—26 November to 10 December 1978; 2) nonmigratory "reds" phase—19 February to 10 March 1979; and 3) migratory "whites" phase—16 November to 9 December 1979.

An area consisting of shallow limestone reefs (6-18 m depth) within 6 km of shore and stretching from Two Rocks Marina to the mouth of Moore River was fished with standard wire beehive pots without escape gaps (Bowen 1971; Morgan and Barker 1974). Pots were baited daily with a variety of fresh fish; heads of Australian salmon, *Arripis trutta*; and bullock hocks.

Tagging Trial A

An experimental area was established, consisting of a grid on which pots were set and undersize lobsters could be displaced distances of 0, 230, 460, 910, 1,370, and 1,830 m from a base line of experimental pots where they were captured (Brown and Caputi 1983). Pots were pulled each morning during the trial, weather permitting. Undersize (66 to <76 mm) lobsters were tagged with a numbered western rock lobster tag (Chittleborough 1974b) and their carapaces measured to the nearest 0.1 mm. Also recorded was the animal's damage, sex, and the depth and bottom type where it was caught and released. Grid areas were generally fished only once to avoid recapturing previously tagged animals. Recaptures of tagged animals were made by commercial fishermen who were paid a reward for the tag and market value for the animal if it had molted to legal size. See Brown and Caputi (1983) for complete details of experimental procedures. Number of releases for this trial was about 1,500.

Tagging Trial B

Procedure for trial B was the same as trial A except that the 1,370 m transect was not set and exposure categories of 0, 30, 60, 120, and 180 min were also examined. Exposed undersize lobster were placed in plastic prawn baskets (lug baskets; commonly used by fishermen to sort their catch) and exposed to air for the desired period before release at one of the displacement transects. About 2,300 tagged animals were released.

Tagging Trial C

Similar procedures were followed as for trials A and B, but only the 1,830 m and a new 3,660 m transects were set and exposure categories of 0, 15, 30, 60 min were used. Because parasite infection was observed on some animals (6.3% of releases), its presence was recorded as it could affect growth. The infection is a combination of a fungus (*Fusarium* sp.) and a bacteria (*Vibrio* sp.), which causes black lesions in the exoskeleton, usually in areas that have been damaged (e.g., tail fans and appendages). Infections were scored on an ordered scale of 0-6, with 0 indicating no infection. About 2,900 tagged animals were released.

Results

Figure 1 shows mean size (carapace) increment related to month of recapture for each of three tagging trials. In tagging trials A and C (November-December releases), February was the first month when there was evidence of molting in animals recaptured (Fig. 1); therefore, subsequent analyses on size increment only used recaptures from February onwards. In tagging trial B (February-March releases), May was the first month when there was evidence of molting (Fig. 1), so only data from this month onwards was used for the analyses.

The results of an analysis of variance (ANOVA) on size increment for each of three tagging trials is shown in Table 1. In this analysis recapture month, sex, color, displacement, and exposure were treated as factors while size at release, damage, and level of parasite infection were treated as covariates. The analysis enables the significance of these factors and covariates to be determined after effects of other factors and covariates are taken into account.

In tagging trial A, after taking the effects of other factors into account (e.g., sex, recapture month, etc.), the size increment per appendage missing was smaller by 0.48 mm with standard error of 0.04. This is also evident from Figure 2 which shows the relationship between mean size increment and numbers of appendages missing for all recaptures from February to June 1979. Size increment in tagging trial C was also smaller by 0.48 mm per appendage missing with standard error of 0.004 (see Figure 3), while that for tagging trial B was 0.33 mm smaller (standard error of 0.07).

From the ANOVA, size increments of displaced compared with nondisplaced animals were smaller by 0.32, 0.65, and 0.27 mm for tagging trials A, B, and C respectively.

Exposure in tagging trial C, after other factors were taken into account by the ANOVA, resulted in increments smaller by 0.83, 1.34, and 2.30 mm for 15-, 30-, and 60-min exposure respectively, when compared with the zero exposure category. This can also be seen from Figure 3 which shows the mean size increment for animals recaptured after February 1980 related to exposure and number of appendages missing. While the effect of exposure on growth was not significant for the February-March 1979 trial B, size increments were smaller by 0.62 and 0.73 mm for 30- and 60-min exposures respectively, compared with unexposed animals.

Mean size increment of males was larger than females by 0.95, 1.34, and 0.76 mm for the three tagging trials. Although the size at release of all animals was between 66 and 76 mm, there was still a highly significant decrease in size increment due to size at release of 0.25, 0.36, and 0.20 mm for every 1 mm increase in size at release. Difference in color, i.e., dark-shelled vs. pale-shelled animals, was significant in tagging trial A with pale-shelled animals having a greater size increment by 0.65 mm, but this was not evident in tagging trial C. In tagging trial C, level of parasite infection of the animals was found to have had a detrimental effect on growth.

DISCUSSION AND CONCLUSIONS

Exposure

Exposing undersize rock lobsters to the atmosphere was detrimental to their growth increment at the first molt after exposure in both laboratory and field tagging trials. In the December laboratory experiment (Group II) the effect of exposure was still significant at the second molt after exposure. Tagging trial B (February-March 1979) resulted in exposure not having a significant effect on growth despite the presence of a negative trend between exposure and size increment. This may have been due to the fact that only 7 of the 110 animals recaptured in May-June 1979 had been exposed; this is the period when many of the undersize lobsters would have undergone their first postexposure molt (Fig. 1). Since there is a closed season from 1 July to 14 November, no recaptures were made until the time of the second postexposure molt in November-December 1979, by which time the combined effects of two molts may have masked the effect of the exposure treatment. However, this was not the case in tagging trial C (November-December 1979), which was held at the start of the fishing season, where the effect of exposure on the first molt which occurs

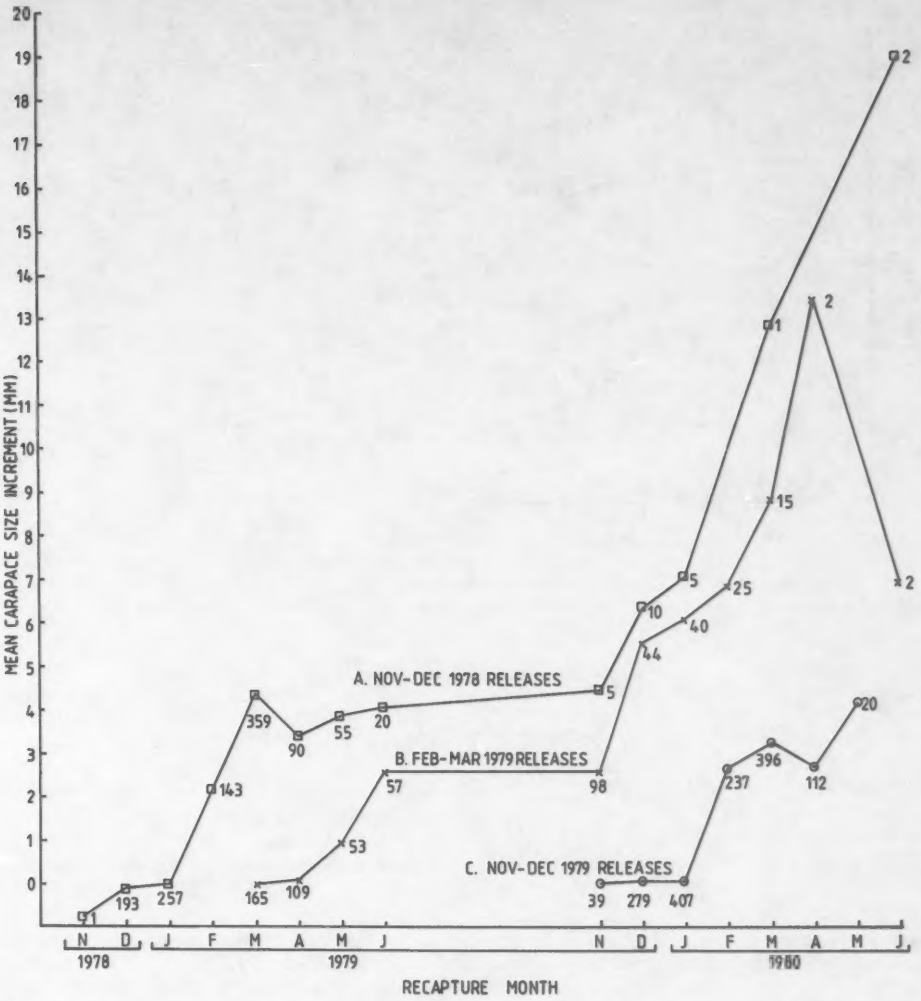
MEAN CARAPACE SIZE INCREMENT (MM)
A. NOV-DEC 1978 RELEASES
B. FEB-MAR 1979 RELEASES
C. NOV-DEC 1979 RELEASES
RECAPTURE MONTH
1978
1979
1980
N D J F M A M J N D J F M A M J

FIGURE 1.—The mean size (carapace) increment by month of recapture and the sample size involved in calculating it shown next to the points, for the three tagging trials at Two Rocks.

around February was clearly evident in animals caught from February 1980 onwards (Fig. 3, Table 1).

Damage

Damage to undersize rock lobsters was clearly shown to have a detrimental effect on growth (Table 1), which was directly proportional to the level of damage (Figs. 2, 3).

Chittleborough (1975) found that growth increment of *P. cygnus* was reduced under laboratory conditions when four or more legs were removed and repetitive loss of two or more limbs led to precocious molting with reduced molt increments leading to an overall reduction in growth. Davis and Dodrill (1980) and Davis (1981) undertook research on the effect of injuries (limb loss) produced by amateur and professional fishermen and natural causes (e.g., predators, molting accidents, etc.) on the growth rate of *P. argus* populations in the wild. They found that

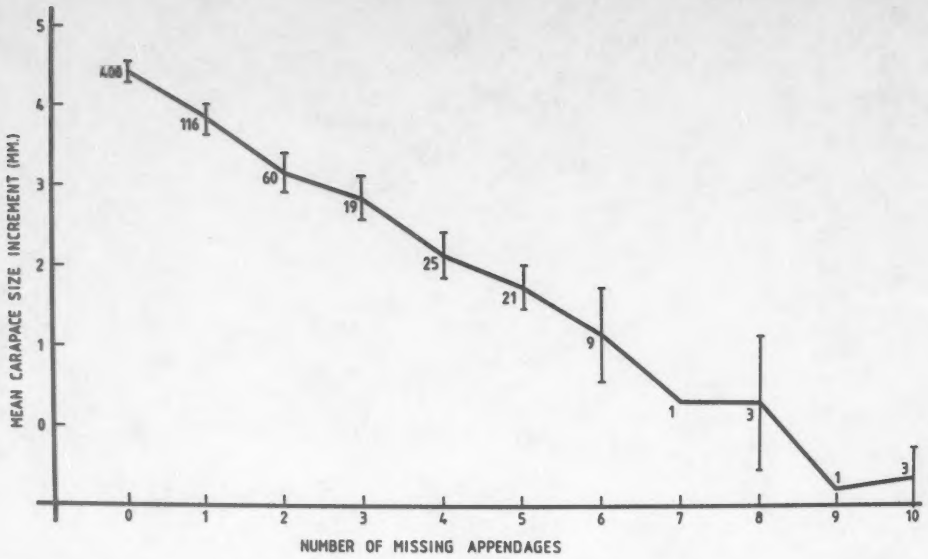

FIGURE 2.—Two Rocks, November-December 1978. The relationship between the mean size increment and number of appendages missing for recaptures from February to June 1979, with the sample size and standard error from the mean shown at each point.

TABLE 1.—The results of the analysis of variance on size increment for the three tagging trials at Two Rocks with the level of significance denoted by: NS, *, **, *** meaning not significant, $P < 0.05$, $P < 0.01$, and $P < 0.001$ respectively, and NA means not applicable.

Factor/covariate	Nov.-Dec. 1978	Feb.-Mar. 1979	Nov.-Dec. 1979
No. missing appendages	***	***	***
Displacement	*	*	*
Exposure	NA	NS	***
Recapture month	***	***	***
Sex	***	***	***
Size at release	***	***	***
Color	**	NA	NS
Parasite infection	NA	NA	***
Sample size	687	335	636

the growth rate of injured animals was significantly lower than that of uninjured animals, due to reductions in molt increment and an increase in intermolt period. Their research did not demonstrate any proportional relationship between the degree of injury and the degree of molt increment depression as had been shown for *H. oregonensis* and *P. crassipes* (Kuris and Mager 1975) and also in this study on *P. cygnus*. Davis (1981) stated that growth rate of *P. argus* with minor injuries, five or fewer appendages missing, was almost identical to the growth rate of more seriously injured animals that were missing up to nine legs and both antennae.

Displacement

The displacement of undersize rock lobster was also found to significantly affect size increment in each of the three tagging trials. This was probably due to movement of animals from their home range (Chittleborough 1974c) which could have interrupted their normal feeding behavior and thus may have contributed to a decrease in food intake and hence growth.

Overall Effect

In general the handling of undersize rock lobsters by fishermen which causes them to be exposed to the atmosphere, damaged and displaced beyond their home range, not only affects their survival (Brown and Caputi 1983) but also affects growth of those that survive. As discussed in Davis (1981), this reduction in growth may result in:

1) The undersize lobsters staying below the legal size for a longer period than necessary with some being subject to natural mortality in this extra period before entering the fishery.
2) Those animals which do enter the fishery would do so at a reduced size, hence harvestable yield would be reduced.

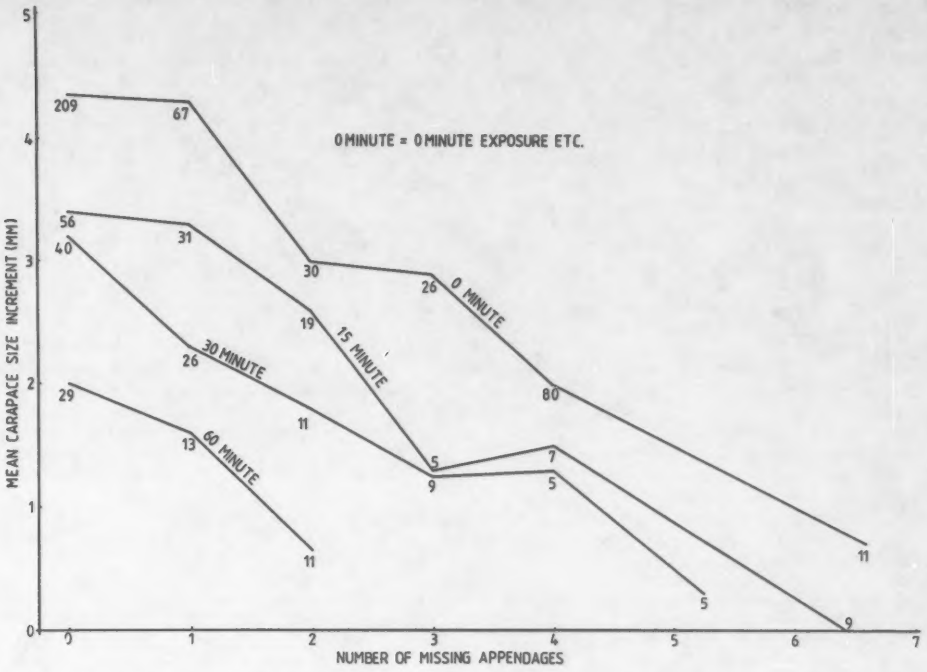

FIGURE 3.—Two Rocks, November-December 1979. The mean size increment related to exposure categories and number of missing appendages for animals recaptured from February 1980 onwards. Exposure and missing appendages categories with less than five individuals have been combined and are plotted at the mean appendage level. The sample sizes are shown next to the points.

3) Size of these animals on reaching maturity would also be reduced, which would cause a decrease in fecundity directly proportional to their reduced size (Morgan 1972). The time they would take to reach maturity would probably not be affected since age appears to determine maturity rather than size (Chittleborough 1974d).
4) Affected animals would remain undersize for longer, thereby increasing the possibility that they could undergo multiple capture and handling. Multiple handling would result in increased mortality and further reduced growth.

These factors, when added to the estimate of 14.6% reduction in recapture rate (most likely due to mortality) of the returned undersize lobsters during the fishing season (Brown and Caputi 1983), constitute a serious loss to the fishery. In addition, any mortality and reduced growth which may occur as a result of lifting the animals to the surface and returning them to the sea would also need to be added to the above loss. This loss could not be quantified as both experimentals and controls in the tagging experiments experienced this.

As mentioned by Brown and Caputi (1983), use of more effective escape gaps and an education program to encourage fishermen to return their undersize rock lobsters immediately to the sea while their vessel remained in the immediate vicinity of where the pot was pulled would help to overcome this serious source of industry created wastage. Both these approaches are currently being examined with a view to reducing the numbers of undersize lobsters that are handled and the time they are kept on board the vessels.

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LITERATURE CITED

AITKEN, D. E.
1980. Moulting and growth. *In* J. S. Cobb and B. F. Phillips (editors), The biology and management of lobsters, Vol. I, p. 91-163. Acad. Press, N.Y.

BOWEN, B. K.
1963. Preliminary report on the effectiveness of escape gaps in crayfish pots. West. Aust. Dep. Fish. Fauna Rep. 2, 9 p.
1971. Management of the western rock lobster (*Panulirus longipes cygnus* George). Proc. Indo-Pac. Fish. Counc. 14(II):139-153.
1980. Spiny lobster fishery management. *In* J. S. Cobb and B. F. Phillips (editors), The biology and management of lobsters, Vol. II, p. 243-264. Acad. Press, N.Y.

BROWN, R. S., AND N. CAPUTI.
1983. Factors affecting the recapture of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Res. 2:103-128.

CHITTLEBOROUGH, R. G.
1974a. Review of prospects for rearing rock lobsters. Aust. Fish. 33(4):4-8.
1974b. Development of a tag for the western rock lobster. CSIRO Div. Fish. Oceanogr. Rep. 56, 19 p.
1974c. Home range, homing and dominance in juvenile western rock lobster. Aust. J. Mar. Freshw. Res. 25:227-234.
1974d. Western rock lobster reared to maturity. Aust. J. Mar. Freshw. Res. 25:221-225.
1975. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshw. Res. 26:177-196.
1976. Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. Aust. J. Mar. Freshw. Res. 27:279-295.

DAVIS, G. E.
1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull., U.S. 78:979-984.

DAVIS, G. E., AND J. W. DODRILL.
1980. Marine parks and sanctuaries for spiny lobster fisheries management. Proc. Gulf. Caribb. Fish. Inst. 32:194-207.

GEORGE, R. W.
1958. The biology of the Western Australian commercial crayfish *Panulirus longipes*. Ph.D. Thesis, Univ. Western Australia, Nedlands, 124 p.

HANCOCK, D. A.
1981. Research for management of the rock lobster fishery of Western Australia. Proc. Gulf. Caribb. Fish. Inst. 33: 207-229.

KURIS, A. M., AND M. MAGER.
1975. Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. J. Exp. Zool. 193:353-359.

MORGAN, G. R.
1972. Fecundity in the western rock lobster, *Panulirus longipes cygnus* (George) (Crustacea:Decapoda:Palinuridae). Aust. J. Mar. Freshw. Res. 23:133-141.
1974. Aspects of the population dynamics of the western rock lobster *Panulirus cygnus* George. II. Seasonal changes in the catchability coefficient. Aust. J. Mar. Freshw. Res. 25: 249-259.
1977. Aspects of the population dynamics of the western rock lobster and their role in management. Ph.D. Thesis, Univ. Western Australia, Nedlands, 341 p.
1980a. Population dynamics and management of the western rock lobster fishery. Mar. Policy 4:52-60.
1980b. Increases in fishing effort in a limited entry fishery - the western rock lobster fishery 1963-76. J. Cons. Int. Explor. Mer 39:82-87.

MORGAN, G. R., AND E. H. BARKER.
1974. The western rock lobster fishery 1972-1973. West. Aust. Dep. Fish. Wildl. Rep. 15, 22 p.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL.
1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull., U.S. 80:475-486.

NORTON, P.
1981. The amateur fishery for the western rock lobster. West. Aust. Dep. Fish. Wildl. Rep. 46, 108 p.

SEA SCALLOP FISHING IMPACT ON AMERICAN LOBSTERS IN THE GULF OF ST. LAWRENCE

G. S. JAMIESON[1] AND A. CAMPBELL[2]

ABSTRACT

Damage to American lobsters, *Homarus americanus*, in Egmont Bay and off Miminegash, Price Edward Island, is minimal from the drags of the seasonal sea scallop, *Placopecten magellanicus*, fishery. During May 1981, when commercial sea scallop fishing was occurring, American lobster abundance was low in areas of profitable scallop exploitation. Sea bed substrate in these areas was generally smooth and most lobsters were able to avoid the gear. In the areas with and without commercial scallop fishing, 1.3% and 11.7% of observed lobsters, respectively, were injured or retained by the drag. Lobster abundance in the areas commercially exploited for scallops in May and June was significantly greater in July than in May, but whether this was a result of a natural seasonal movement of lobsters or the cessation of scallop fishing is unclear.

Sea scallop, *Placopecten magellanicus*, and American lobster, *Homarus americanus*, populations are fully exploited in Northumberland Strait, Gulf of St. Lawrence (Wilder 1947, 1965; Robinson 1979; Jamieson et al. 1981c; Campbell and Mohn 1983). Individual fishermen frequently fish both species, commonly in the same general area, although the fisheries are separated temporally (Jamieson et al. 1981c; Conan and Maynard 1983). Recently, localized low abundance of these important, commercial species has heightened long-held convictions by fishermen of the negative impact of sea scallop fishing on American lobster stocks. Fishermen's concern became acute for the Egmont Bay area during 1980, coincident with the discovery and exploitation of new nearshore scallop concentrations near West Point, Prince Edward Island (Fig. 1). Decreased scallop recruitment in recent years (Jamieson et al. 1981b, c) has resulted in a scarcity of scallops in traditional fishing areas, causing increased exploration for commercially exploitable scallop concentrations.

The magnitude of scallop gear-lobster interaction is dependent on the spatial and seasonal distributions of scallops and lobsters and the impact of scallop gear on commercial lobster abundance where the distributions of both species overlap. Scallops are widespread in Northumberland Strait (Caddy et al. 1977), but commercial concentrations are found only in limited areas. The precise locations of these areas are undocumented, and since they vary with time, they cannot be predicted with any accuracy. However, commercial log data has shown the broad distribution of scallop concentrations in Northumberland Strait during 1979-80 (Jamieson et al. 1981b, c).

The seasonal abundance and distribution of commercial-sized lobsters is largely unknown, but their general distribution overlaps that of scallops (Stasko et al. 1977; Conan and Maynard 1983). There have been few field studies conducted on lobsters in this area: Templemann (1933, 1934, 1935, 1936) reported on lobsters and the fishery in Northumberland Strait; Wilder (1963) and Wilder and Murray (1956) reported on movements and growth of tagged lobsters liberated in Egmont Bay.

Scallop and Irish moss, *Chondrus crispus*, drags can damage lobsters, although lobsters exposed on open ground tended to avoid moving drags. Most gear-induced damage has resulted from lobsters in burrows being hit or crushed by rocks disturbed by the drag (Scarratt 1973, 1975; Pringle and Jones 1980).

Investigations reported here document 1) the scallop drag/lobster interactions off Miminegash, Prince Edward Island, during August 1978 and in Egmont Bay during May and July 1981; and 2) the relative abundance and movement of lobsters trapped and tagged in Egmont Bay prior to (June-July 1981) and during the lobster fishing season (10 August-10 October 1981). Lobster abundance may change relatively rapidly because of their potential high mobility. Therefore it is important to characterize lobster microdistribution and assess the con-

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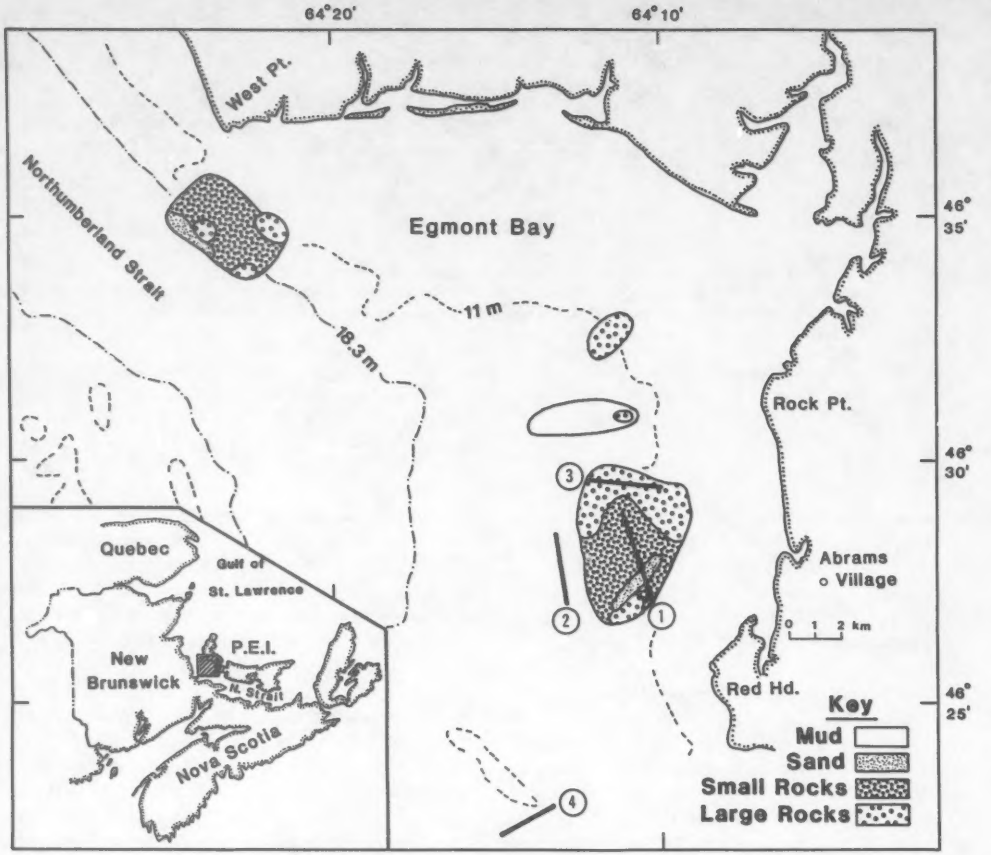

FIGURE 1.—General substrate type as observed by divers in the areas surveyed in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Locations of stations (heavy lines) sampled for lobsters in Egmont Bay, Northumberland Strait: 1 = recently heavily fished scallop ground, 2 = recently lightly fished scallop ground, 3 = no recent scallop fishing (large rocks), 4 = no scallop fishing (deeper water).

sequences of scallop fishing on the degree of species overlap. Scallop fishing may directly damage lobsters, or because of the disturbance of the sea bed by the drags, may cause lobsters to avoid or be attracted to the overall area.

METHODS

Scallop Gear-Lobster Interactions

1978 Study

The interaction between three types of scallop gear and lobsters was observed by divers between 15 and 30 August 1978. The study area was in 14 m of water about 1 km from shore (long. 46°52′30″W, lat. 64°14′00″N), and consisted of a sandy bottom with occasional small rocks. The gear used was a two-gang, toothed Gulf rock drag (60 cm buckets) (Fig. 2); a two-gang Digby rock drag (76 cm buckets, no teeth) (MacPhail 1954); and a 152 cm Gulf sweep chain drag. A Gulf sweep chain drag is a smaller, lighter revision of an offshore scallop drag (Bourne 1964). A hood of 38 mm stretch mesh was placed over the drags extending to a height of 81 m above the sea bottom, and one of the buckets (half the chain sweep drag) had a similar mesh hood on the outside of the back of the drag (back cover). The bucket, or portion of the drag, without a back cover had a mesh liner. Two divers hung onto each drag during tows,

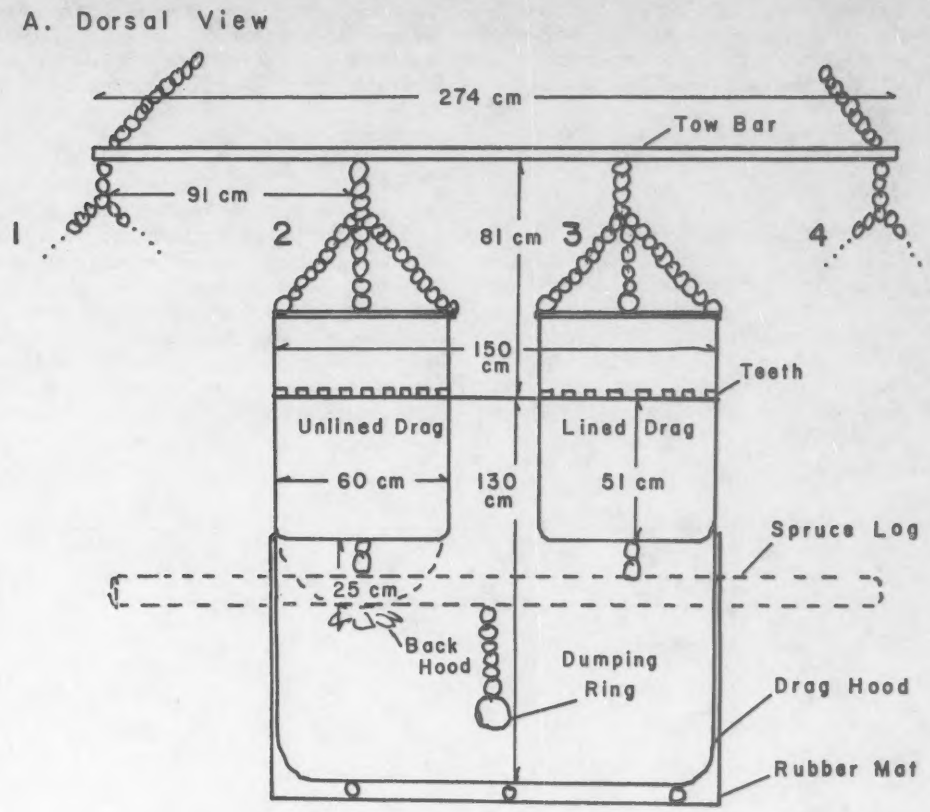

FIGURE 2.—Schematic drawings of a four-gang Gulf rock drag: (A) hood and liner arrangements used with buckets 2 and 3 in 1978 (buckets 1 and 4 were removed). In 1981, 4 unmodified buckets were used. (B) Lateral view of bucket 2 used in 1978.

noting lobster behavior and the physical effect of the drag on lobsters; carapace lengths (CL, back of eye socket to posterior carapace margin) of fished lobsters were measured. Tow velocities, established by engine rpm, were similar to commercial operations and tow duration was 5 min.

1981 Study

Dragging was conducted during 14-22 May and 27-31 July 1981. Four general areas (Fig. 3) were surveyed in both periods. Scallops and lobsters were known by fishermen to exist in areas A and A′ but scallop fishing had not occurred for several years; five research tows were conducted in May and three tows in July. Areas B and C were reported by fishermen to be prime lobster ground where scallop fishing had occurred recently or was in progress during the study; 30 research tows were conducted in May and 25 tows in July. Tow locations were randomized within an area and the number per area was arbitrarily assigned according to the apparent distribution of commercial effort in the scallop fishery. Bottom water temperatures averaged 8.8° and 18.4°C in May and July, respectively. A four-gang Gulf rock drag (Fig. 2) with 51 cm buckets was used throughout the study. Scallop rings had 69-75 mm and 80-84 mm inside and outside diameters, respectively. Lead ropes 30 m long were attached to each end of the 2.36 m club stick at the back of the drag to define an area behind the drag to be surveyed by divers. Before the drag was dropped, the lines were let out while the vessel was steaming or drifting to establish an unfished control area for survey

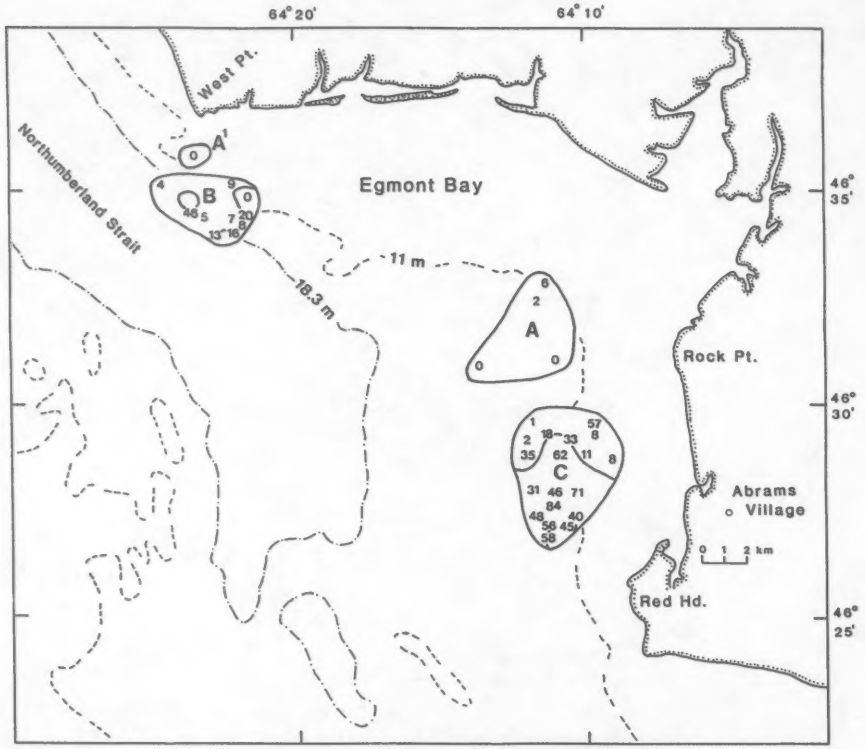

FIGURE 3.—Number of scallops fished/tow (average length = 975 m) by the gear in May in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Identified areas are where both scallops and lobsters exist in commercial densities: A and A′ were areas where no scallop fishing had occurred for several years (= unfished control); B and C were areas where scallop fishing had recently occurred or was in progress during the study. Substrate type is shown in Figure 1.

by the divers when the drag was finally lowered. When the drag was on the bottom, divers swam along the outside edge of each lead line with a 2 m rod, noting all scallops and lobsters encountered in the 2 m wide unfished "path" (120 m^2). The divers then positioned themselves on the drag and noted the number of lobsters in the drag path during the tow, which covered on average 975 m (SD = 221). When the tow terminated, the divers searched the drag path between the lead lines (70.8 m^2) and collected the scallops and lobsters encountered. Scallop height (edge of hinge to distal edge of the valves) and lobster carapace lengths were measured to the nearest millimeter with a measuring board and vernier calipers, respectively. Location (loran C readings), bottom type (Fig. 1), water temperature, and marine plant presence were noted. Tow distance and speed were calculated from loran C readings (Jamieson 1982) and averaged 4.6 kn (SD = 1.9) in May and 4.3 kn (SD = 1.7) in July. Average tow duration was 6.9 min.

Lobster Abundance and Distribution

Four study areas (Table 1; Fig. 1) were located by loran C and were selected after bottom types were characterized from scuba diving observations. The areas were 1) recently heavily fished scallop ground, 2) recently lightly fished scallop ground, 3) ground with large rocks with no recent scallop fishing, and 4) typical lobster ground in waters deeper than areas 1-3 with no scallop fishing. Fifty, three bow, single kitchen and parlor design lobster traps with 121 mm diameter entrance ring and 31-34 mm lath spaces were set in each area. Each trap was baited with salted gaspereau (or alewife), *Alosa pseudoharengus*, and/or Atlantic herring, *Clupea harengus harengus*. The traps were set in groups, two traps per buoy, within a 1 km radius of the center of the area (Table 1). The mean interval between trap hauls from 22 June to 30 July was 3 d (1-7 d range). Each trap was reset as close as possible to the original site of each trap set.

The sex and carapace length (CL in mm) of each trapped lobster was recorded. Once a week, the terminal quarter of a pleopod endopodite was removed with scissors from each of 70-140 lobsters of various size groups, and placed in a vial containing seawater. The pleopod method described by Aiken (1973) was used to determine the molt stage of each lobster.

The bottom and surface water temperatures were recorded for each area and time fished. To observe lobster movement and growth, a total of 2,002 lobsters (ca. 500 lobsters/area) were measured and tagged (Table 1) with a sphyrion tag (Scarratt and Elson 1965) and returned to the water within 10 min and 0.5 km of the capture site. During the 10 August-10 October fishing season, lobster samples were obtained at-sea from commercial lobster fishing boats at a number of locations within and near areas 1-4.

One-way analysis of variance was used to compare the mean number of lobsters per trap haul in each area during a 1-wk sampling period and to compare the mean distance moved for lobsters from the different study areas.

From tagged lobsters recaught during the study, movement and direction statistics of tagged lobsters were analyzed by methods Jones (1959) and Saila

TABLE 1.—Summary of Egmont Bay lobster tagging experiment, 22 June-30 July 1981.

Details	Area 1 Heavily fished scallop ground	Area 2 Lightly fished scallop ground	Area 3 Scallop ground with rocks[1]	Area 4 Lobster ground[1]
Location				
Latitude (°N)	46°28′	46°27′	46°28′	46°23′
Longitude (°W)	64°10′	64°13′	64°12′	64°15′
Bottom type	mud, small rock (<10 cm)	mud, small rock (<10 cm)	mud, rocks (>10 cm)	mud, rocks (>10 cm)
Mean depth (m)	11	13	11	18
No. of traps	50	50	50	50
Trap soak-over (days) (range)	2-5	1-7	2-5	1-5
No. of trap hauls	489	568	500	591
No. of lobsters caught	2,507	1,967	2,568	2,330
Total tags released	500	501	500	501
Total tags returned[2]	182	162	234	162
% of total tags released in area[2]	36.4	32.3	46.8	32.3

[1]No scallop fishing.
[2]Number of tags returned up to 30 October 1981 including tags without recapture locations.

and Flowers (1968) have reported, using a computer program by Campbell et al. (1983).

RESULTS

Scallop Gear-Lobster Interactions

1978 Study

No scallops were present but lobsters were numerous and were observed by divers to be frequently foraging in the open. Average carapace length of 22 diver-collected lobsters was 61.3 mm (SD = 26.8). While the microdistribution of substrate type was patchy, tows were of sufficient duration to cover all substrate types. Under the assumption of an average uniform lobster density during tows, lobster catches made by the Gulf sweep-chain drag over sand and rock-sand were highest. Average catches in the lined and unlined portion of the drag were 0.53 and 0.07 lobsters/m of drag width fished per min ($m^{-1}min^{-1}$), respectively (Table 2).

No lobsters were retained by the unlined rock drags, but since they were retained in the back cover of the drag, lobsters were entering the drag and passing through the rings. These lobsters did not show any external evidence of damage. The hoods of all three drag types contained lobsters, indicating that lobsters can escape by swimming over the advancing drag.

TABLE 2.—Average number of lobsters caught $m^{-1}min^{-1}$ of drag width in the hoods and linings of the scallop gear used in 1978. Each drag type was hauled over both sand and sand-rock substrates off Miminegash, Prince Edward Island. L = lined gear; UL = unlined gear; H = hood; B = back cover.

Drag type	No. tows	Lobster catch L	UL	H	B
Gulf sweep chain	5	0.53	0.07	0.15	0.31
Gulf rock drag	5	0.11	0.00	0.06	0.11
Digby rock drag	6	0.02	0.00	0.07	0.04

1981 Study

RELATIVE SCALLOP AND LOBSTER ABUNDANCE.—Catch results and sightings per tow (Jamieson et al. 1981a) indicated that for each study area, considerable variation existed in abundance of both scallops (Fig. 3) and lobsters (Fig. 4). Substrate type was variable over the distance of a single tow, and this appeared to be a major factor influencing relative scallop and lobster abundance.

Scallop and lobster densities in the two areas (B and C) fished for scallops varied significantly on some dates (Table 3) from those densities in the nonfished areas (A and A[1]); fished grounds had a greater number of scallops, but fewer lobsters, than did the nonfished ground. Between the two fished areas, the only significant ($P < 0.05$) difference was in the scallop drag catch in May, but study area C off Red Head generally yielded more of both species than did study area B off West Point (Figs. 3, 4).

There were no significant differences ($P > 0.05$) in the densities of either scallop or lobster in the nonfished area between the two sampling periods. Lobster sightings per tow in both fished areas were significantly greater ($P < 0.05$) in July than in May, but the number of sightings averaged less than in the unfished area. Although not always significant, the general seasonal trend of lobster abundance, as indicated by the control sampling procedures, increased between May and July in all areas. Scallop catch decreased significantly ($P < 0.01$) in the ground off Red Head between May and July. On fished ground, average scallop density decreased whereas scallop density on the nonfished ground increased during this time period.

TABLE 3.—Average scallop and lobster catch in a 4-gang Gulf rock drag in 1981, and the abundance per 1,000 m^2 in each study area before the scallop drag was towed (control) and in the drag path behind the drag. Values with asterisks are significantly different from the corresponding value in the nonfished scallop location. * = $P < 0.05$; ** = $P < 0.01$; n = number of tows.

		Control density				Drag				Drag path			
Location	Month	n	Scallop	n	Lobster	n	No. scallop caught	n	No. lobsters observed	n	Scallop	n	Lobster
Nonfished area	May	4	6.25	4	2.08	5	0.87	4	3.03	2	0.0	2	0.00
	July	2	12.50	2	16.67	3	0.15	3	4.62	3	4.71	3	4.71
West Point	May	4	56.23	4	0.00	11	7.59*	11	0.48	8	24.70*	8	1.76
	July	3	22.21	3	2.78*	7	10.10	7	1.48*	5	127.08	5	5.65
Red Head	May	9	99.03**	9	0.93	19	16.38**	19	0.87	12	68.25**	12	1.18
	July	9	58.31	9	5.55	18	8.34**	18	1.98*	10	52.24	10	1.41

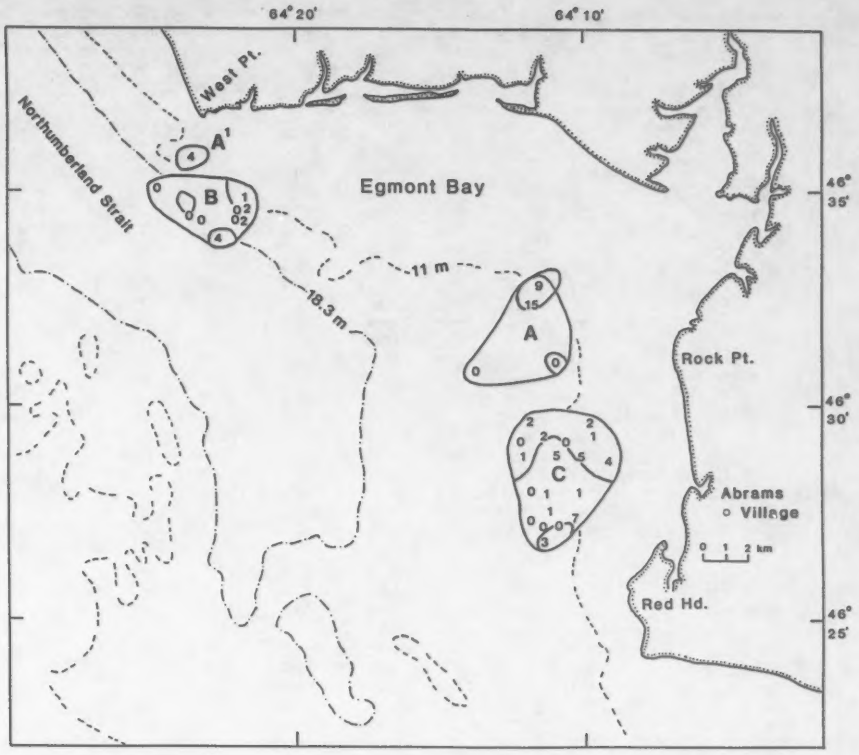

FIGURE 4.—Number of lobsters observed by divers in May during each tow in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Substrate type is shown in Figure 1. Area designations are explained in Figure 3.

SCALLOP GEAR: LOBSTER INTERACTION.—No relation was found between the two sample periods and the number of lobsters injured or retained during a tow (Table 4). The weighted percentage of lobsters injured or retained was 11.7 and 1.3, for the nonfished and combined fished areas, respectively. Injured lobsters were not found in the drag path, although occasionally lobsters were observed to retreat into burrows in front of a moving drag. Whether they subsequently became damaged or trapped in their burrows is unknown, but the absence of damaged lobsters in the drag path suggests that the frequency of lobster damage is low on commercial scallop ground especially where there is a general lack of large rocks and boulders. However, 14 of the 30 locations surveyed had occasional large rocks.

Most lobsters encountered were too small (mean CL = 72 mm) (Table 5) to be retained by the scallop gear unless the steel rings making the drag were partially blocked by debris. All lobsters <92 mm CL can pass through a 70 mm inside diameter scallop ring (Stasko 1975). Several lobsters were seen by the divers entering the drag and passing through the rings apparently unscathed. In 63 tows, 11 lobsters were affected directly by the scallop gear: four were retained by the drag (the ring openings were block-

TABLE 4.—Frequency by month and location of lobster reduction and/or injury during dragging.

Details	Month	Nonfished areas	Fished areas	
			West Point	Red Head
No. lobsters observed	May	28	10	35
	July	32	24	82
No. lobsters injured/retained	May	3	1	0
	July	4	1	0
% injured/ retained	May	11	10	0
	July	13	4	0

TABLE 5.—Summary of lobster catches during closed fishing season (June-July 1981) and during the fishing season (August-October 1981) in Egmont Bay. Shorts = prerecruits <63.5 mm CL; legals = recruits ≥63.5 mm CL.

					Prerecruits			Recruits		
Week no.	Time period	Area	No. of lobsters sampled	No. of trap hauls	% total lobsters	No. per trap haul	% females of total shorts	No. per trap haul	% females of total legals	Mean CL (mm)
1	22-26 June	2	2	104	0	0	0	0.02	0	81.0
		4	2	96	50.0	0.01	0	0.01	100.0	72.0
2	29 June-	1	3	100	33.3	0.01	100.0	0.02	100.0	71.0
	3 July	2	17	102	29.4	0.05	80.0	0.12	33.3	68.8
		3	2	100	50.0	0.01	100.0	0.01	100.0	66.0
		4	11	100	45.5	0.05	40.0	0.06	50.0	67.3
3	6-10 July	1	141	98	9.2	0.13	53.9	1.31	20.3	71.4
		2	114	102	12.3	0.14	35.7	0.98	35.4	71.5
		3	99	100	11.1	0.11	72.7	0.88	21.6	70.9
		4	35	100	25.0	0.09	22.2	0.27	30.8	72.6
4	13-17 July	1	503	94	17.7	0.95	42.7	4.40	31.9	71.0
		2	542	104	10.4	0.59	54.1	5.06	33.8	72.1
		3	550	100	12.2	0.67	41.8	4.83	33.3	71.3
		4	395	100	9.4	0.38	45.9	3.65	31.6	72.6
5	20-24 July	1	794	99	13.7	1.10	55.0	6.92	33.9	69.9
		2	708	104	9.0	0.62	51.6	6.19	36.3	71.6
		3	840	100	10.7	0.90	47.8	7.50	36.6	70.4
		4	792	98	6.3	0.51	58.0	7.57	33.8	72.4
6	27-30 July	1	1,066	98	15.7	1.70	44.3	9.17	29.1	70.3
		2	584	52	9.3	1.04	57.4	10.19	31.0	71.6
		3	1,077	100	9.2	0.99	44.4	9.78	29.6	70.9
		4	1,095	97	6.2	0.70	39.7	10.59	32.0	73.3
8	10-14 Aug.	(1)	1,582	488	24.5	0.79	44.9	2.40	33.1	71.9
9	17-21 Aug.	(1)	155	125	47.7	0.59	46.2	0.65	(2)	(2)
10	24-28 Aug.	(1)	501	240	44.7	0.93	48.5	1.13	31.8	73.2
11	13 Aug.-									
	4 Sept.	(1)	458	245	42.5	0.80	42.6	1.07	34.4	73.0
13	14-18 Sept.	(1)	496	237	51.6	1.08	50.8	0.99	44.2	71.5
15	28 Sept.-									
	2 Oct.	(1)	129	74	7.7	1.18	53.4	0.57	(2)	(2)

[1]All fishing areas during fishing season.
[2]Size and sex not recorded

ed with *Laminaria longicruris*), four passed under the drag and were possibly injured, and three were struck during the course of one tow (in May) resulting in claw loss or a cracked carapace. In the latter instance, strong currents impeded the escape of lobsters.

Scallop size frequencies were similar in May and July in each of the two commercially fished areas and all scallop age classes were exploited about equally.

Lobster Abundance and Distribution

Abundance

The number of lobsters caught per unit of effort (trap haul; CPUE) increased during the experimental fishing period in all areas (Table 5). During the commercial fishing period, CPUE of prerecruits increased but CPUE of legal-sized lobsters decreased presumably as a result of fishing mortality. Number of lobsters per trap haul was not significantly different between areas observed during the experimental period (Table 5). The use of CPUE is unreliable in the quantitative estimation of lobster abundance as many factors affect trapability, including water temperature, lobster behavior, molting, relative trap and lobster densities, and bait attractiveness (Elner 1980).

Lobster Movement

Of the 740 tagged lobsters recaptured (37%), 658 had recapture location data (Tables 1, 6). In areas 1, 2, and 3, the majority (65-78%) of tagged lobsters were recaptured within 10 km of release, but in area 4, 50% were caught 11-18.5 km from release (Table 6). The mean distance moved was not significantly different for tagged lobsters released in areas 1, 2, or 3, but lobsters from area 4 moved a significantly ($P < 0.01$) greater mean distance than those of the other three areas.

Direction statistics (according to Saila and Flowers 1968) summarize the nature of lobster movement

TABLE 6.—Summary statistics of distance travelled and direction moved by tagged lobsters released at four areas in Egmont Bay during June-July 1981, and recaptured up to 30 October 1981. (Direction statistics calculated according to Jones [1959] and Saila and Flowers [1968] are $\bar{\theta}$ = mean vector angle from true north; V and V′ = directed movement along north-south and east-west plane, respectively, negative values of V and V′ indicate net southerly and westerly movement, respectively; R and Z = Rayleigh test statistics for randomness or uniform distribution of points about a circle; * = significant at $P < 0.01$ indicates a non-uniform distribution.) SD = Standard deviation.

	Release area			
Details	1 Heavily fished scallop ground	2 Lightly fished scallop ground	3 Scallop ground with rocks[1]	4 Lobster ground[1]
% of total recaptures moved 0-10 km	65.2	70.3	78.2	35.3
% of total recaptures moved 11-18.5 km	28.1	16.2	19.8	49.7
% of total recaptures moved >18.5 km	6.7	13.5	2.0	15.0
Total recaptures	164	148	207	139
Mean distance moved, km (±1 SD)	9.2 (0.5)	10.1 (0.6)	8.3 (0.4)	[2]12.9 (0.6)
Maximum distance moved, km	25.0	45.0	38.9	49.7
$\bar{\theta}$	247.3	289.3	310.5	344.4
V (km/d)	−0.055	0.026	0.062	0.213
V′ (km/d)	−0.132	−0.075	−0.073	−0.059
R	74.9	26.3	64.9	63.5
Z	34.2*	4.7*	20.4*	29.0*

[1]Light or no scallop fishing.
[2]Value for mean distance travelled significantly different ($P < 0.01$); other values not significantly different ($P > 0.05$).

(Table 6). The Rayleigh test statistic, Z, indicated a non-uniform distribution of tag returns ($P < 0.01$) for each area of release. Results of the Rayleigh test should be treated with caution (Batschalet 1965) since there is some evidence of bimodality. In general, the returns exhibited three main directions of movement for lobsters: south-west for area 1, north-west for areas 2 and 3, and north for area 4 (Table 6). V and V′, the north-south and east-west coefficients of directed movement, measure the mean daily travel of the group. Lobsters from areas 1-3 showed little dispersion in a north-south direction in contrast to lobsters from area 4, which moved the greatest in a northward direction (0.213 km/d). Lobsters from all areas generally moved west, but lobsters from Area 1, the heavily fished scallop ground, tended to disperse furthest west per day (0.132 km/d). Dispersion to the west is perhaps largely the result of the relative proximity of the release areas to the western shore of Prince Edward Island, which restricted lobster movement to the east.

Lobster Growth

Determinations of molt stage from pleopod examinations indicated that lobsters may have molted as early as 6-12 July (Table 7). Trapability of lobsters is affected by molt stage, with late molt stages (e.g., $D_{4.0}$; Aiken 1973) being difficult to trap. The high percentage of D_3 to D_4 animals (stages just before molting) in mid-August indicated that considerable molting was imminent, and this probably affected CPUE at this time. Many tagged lobsters (47.8%, $N = 46$) recaptured during the period 24 August-26 September had molted.

DISCUSSION

The results of this study are probably area and

TABLE 7.—Percentage of pleopod stages of lobsters sampled from Egmont Bay, July-September 1981. Pleopod stages 3.0-3.5 and 4.0-5.5 predict lobsters molting within 1.9-4.0 wk and 0.3-2.4 wk, respectively, at 15°-19°C (Aiken 1973). Prediction of molting time for pleopod stage 1.0-2.5 is unreliable but usually exceeds 4.0-10.3 wk.

	% of lobsters				
	Pleopod stage				
Period	1.0-2.5	3.0-3.5	4.0-5.5	No. of lobsters	Temperature (°C)
6-10 July	97.1	1.5	1.4	69	15.5
13-17 July	98.2	0.9	0.9	113	16.0
20-24 July	96.5	3.5	0.0	142	16.5
27-30 July	89.9	6.6	3.5	117	19.0
10-14 Aug.	76.3	21.1	2.6	76	18.1
31 Aug.-4 Sept.	91.1	5.9	3.0	101	17.5

time specific. Nevertheless the extent of sea scallop gear damage to American lobsters in Egmont Bay was measured, and this permits estimation of the damage to lobsters on similar substrate types in other locations. In the nonfished area there was no significant difference in the lobster abundance between the May and July observations, whereas there were significant differences in relative seasonal lobster abundance in the fished areas. In western Northumberland Strait at the time of this study, scallop fishing occurred primarily between late April and late June, with a minor amount of fishing between mid-October and winter freeze-up (Jamieson et al. 1981c). There was limited scallop fishing during July. If lobsters were displaced by scallop dragging during May and June, normal seasonal lobster densities could be reestablished by late July. It is unclear whether the greater density of lobsters in the fished areas in July was due to normal seasonal migration onto these grounds or to the absence of scallop fishing. Data from tagged lobsters suggested that some immigration may have occurred from the deeper water areas of the Strait, but it also appeared that overall abundance on the scallop grounds may have been reduced by scallop dragging activity. Predators have been reported to be attracted to the disturbed substrate in a drag's path (Caddy 1973), but how this relates to lobsters is unclear.

The trapability of lobsters is a function of many variables (Elner 1980), making the quantification of lobster abundance difficult in the four trap study areas. There was a lower percentage of short lobsters and a larger mean carapace length in Area 4 than in the other areas (Table 5). When large lobsters were trapped there were generally fewer small lobsters in the traps (Table 5), but this may have resulted from agonistic behavior (Cobb and Tamm 1975) rather than relative density. Water temperature increases may also have affected behavior and possibly had major modifying effects on lobster growth and/or movement. McLeese and Wilder (1958) documented an increase in lobster rate of movement with increasing temperature, but what effect this had on the average direction of movement during the study period is unclear. The mean movement rate of lobsters in our study (Table 7) was similar to that reported by Saila and Flowers (1968) for mature lobsters off Rhode Island. Saila and Flowers (1968) showed that the coefficients of directed movement, V and V′, are sensitive to changes in movement patterns at various life history stages, and hence are a possible function of lobster maturity level and the sex ratio used in their calculation. These potential influences were not considered here because of limited duration of the study and the relative close proximity of release and recapture areas which were probably not optimal to permit extensive data analysis.

There probably was a directed movement of tagged lobsters from area 4 (deeper water) into Egmont Bay. This may have contributed to the increased CPUE during July-October. Templeman (1936) found there was some movement during the summer with lobsters congregating in the relatively shallow inshore water areas of Northumberland Strait and that some lobsters moved offshore in the fall. The disproportionate sex ratio of legal-sized lobsters observed in the present study suggested a geographic distributional difference between the sexes of lobsters after maturity during July-August.

Lobster trapability, and hence estimated abundance, can be influenced by molt stage. Many legal-sized lobsters appeared to have molted between August and September, and while the data are insufficient to support the fact that a molt may have occurred prior to or during the experimental fishing period (late June-July), other investigations have presented evidence in the literature that lobsters in this area do molt in late spring (Templeman 1934, 1936; Wilder 1963). If, in fact, two molts did occur during the study period, this along with increased water temperature increasing lobster movement (McLeese and Wilder 1958) could partially explain the rapid increase in CPUE during July. However, no soft-shelled lobsters were observed during July, while soft-shelled lobsters were quite frequently encountered in fishermen's traps during the August-September fishing season.

The seasonal nature of the fisheries minimizes the impact of scallop gear on lobsters because lobsters are in low abundance on scallop ground at the time of greatest scallop fishing activity. Commercial concentrations of scallops and lobsters also appear to be largely separated spatially (Figs. 2, 3). What then is the likely economic impact in Egmont Bay of scallop fishing on lobsters, and how does this compare to the value of the exploited scallop resource? No reported commercial scallop fishing was reported in 1980 off Red Head, but vessel logs recorded that 1,509.4 kg of adductor muscle meat were taken near West Point (scallop log areas 77 and 78 combined, Jamieson et al. 1981c). Average CPUE was about 2.4 $kg/h \cdot m^{-1}$, indicating that 629 $h \cdot m$ of effort was expended. In our study, a total of 8.2 $h \cdot m$ of research effort was expended in May on the fished grounds and 22 lobsters were observed behind the drag in the drag path. Drag velocities over the bottom in

both commercial fishing operations and in our study are assumed to be similar. If 2.6% of the lobsters observed are retained or injured, with 50% of these lobsters killed, then the total number of lobsters estimated to be destroyed by commercial scallop fishing in 1980 was 22 lobsters. If each lobster weighed 0.5 kg and was valued at \$6.60 kg^{-1}, then the loss would be about \$73. In comparison, at \$8.27 kg^{-1} of scallop meat in May, 1980 (Jamieson et al. 1981c), the scallop landings from these two fished areas had an estimated value of \$12,483.

If lobster abundance was as high as that in the unfished area, i.e., 3.03 lobsters/1000 m^2, then 139 lobsters, with a value of \$460, would have been destroyed. In both instances, this loss is negligible in comparison to the values of the lobster and scallop fisheries. These conclusions are in agreement with the observations of Scarratt (1973) and Pringle and Sharp (1980) in their assessments of the impact of Irish moss raking on lobster populations.

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LITERATURE CITED

AIKEN, D. E.
1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30:1337-1344.

BATSCHALET, E.
1965. Statistical methods for analysis of problems in arrived orientations and certain biological rhythms. Am. Inst. Biol. Sci., 54 p.

BOURNE, N.
1964. Scallops and the offshore fishery of the Maritimes. Fish. Res. Board Can. Bull. 145, 60 p.

CADDY, J. F.
1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. J. Fish. Res. Board Can. 30:173-180.

CADDY, J. F., T. AMARATUNGA, M. J. DADSWELL, T. EDELSTEIN, L. E. LINKLETTER, B. R. MCMULLIN, A. B. STASKO, AND W. H. VAN DEPOLL.
1977. 1975 Northumberland Stait project, Part I. Benthic fauna, flora, demersal fish and sedimentary data. Can. Fish. Mar. Serv., MS Rep. 1431, 46 p.

CAMPBELL, A., S. E. BELLIS, G. E. FAWKES, AND C. HASTEY.
1983. Computer programs for analysis of lobster (*Homarus americanus*) movements from tag-recapture data. Can. Ms. Rep. Fish. Aquat. Sci. 1705, 22 p.

CAMPBELL, A., AND R. K. MOHN.
1983. Definition of American lobster stocks for the Canadian Maritimes by analysis of fishery-landing trends. Trans. Am. Fish. Soc. 112:744-759.

COBB, J. S., AND G. R. TAMM.
1975. Dominance status and molt order in lobsters (*Homarus americanus*). Mar. Behav. Physiol. 3:119-124.

CONAN, G. Y., AND D. R. MAYNARD.
1983. Aerial survey of spatial distribution of effort in lobster fishery of southern Gulf of St. Lawrence. ICES Shellfish Committee CM 1983/K 13, 14 p.

ELNER, R. W.
1980. Lobster gear selectivity-A Canadian overview. *In* V. C. Anthony and J. F. Caddy (editors), Proceedings of the Canada-U.S. workshop on status of assessment science for N. W. Atlantic lobster (*Homarus americanus*) stocks, St. Andrews, N. B., Oct 24-26, 1978, p. 77-83. Can. Tech. Rep. Fish. Aquat. Sci. 932.

JAMIESON, G. S.
1982. A system for the precise determination of tow distance and tow path in offshore resource surveys. Can. Tech. Rep. Fish. Aquat. Sci. 1035, 34 p.

JAMIESON, G. S., M. ETTER, AND R. A. CHANDLER.
1981a. The effect of scallop fishing on lobsters in the western Northumberland Strait. CAFSAC Res. Doc. 81/71, 19 p.

JAMIESON, G. S., N. B. WITHERSPOON, AND M. J. LUNDY.
1981b. Assessment of Northumberland Strait scallop stocks - 1979. Can. Tech. Rep. Fish. Aquat. Sci. 1013, 31 p.
1981c. Assessment of Northumberland Strait scallop stocks - 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1017, 44 p.

JONES, R.
1959. A method of analysis of some tagged haddock returns. J. Cons. Perm. Int. Explor. Mer 25:58-72.

MACPHAIL, J. S.
1954. The inshore scallop fishery of the Maritime Provinces. Fish. Res. Board Can., Atl. Biol. Stn. Circ., Gen. Ser. No. 22, 4 p.

MCLEESE, D. W., AND D. G. WILDER.
1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. J. Fish. Res. Board Can. 15:1345-1354.

PRINGLE, J. D., AND D. J. JONES.
1980. The interaction of lobster, scallop, and Irish moss fisheries off Borden, Prince Edward Island. Can. Tech. Rep. Fish. Aquat. Sci. 973, 10 p.

PRINGLE, J. D., AND G. J. SHARP.
1980. Multispecies resource management of economically important marine plant communities of eastern Canada. Helgol. wiss. Meeresunters. 33:711-720.

ROBINSON, D. G.
1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis; with special reference to the Canso Causeway. *In* F. D. McCracken (editor), Canso Marine Environment Workshop Part 3 of 4 Parts Fishery Impacts, p. 77-99. Can. Fish. Mar. Serv., Tech. Rep. 834.

SAILA, S. B., AND J. M. FLOWERS.
1968. Movements and behavior of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. Int. Explor. Mer 31:342-351.

SCARRATT, D. J.
1968. 1973. The effect of raking Irish moss (*Chondrus crispus*) on lobsters in Prince Edward Island. Helgol. wiss.

Meeresunters. 24:415-424.
1975. Observations on lobsters and scallops near Pictou, N.S. Can. Fish. Mar. Serv., Tech. Rep. 532, 6 p.

SCARRATT, D. J., AND P. F. ELSON.
1965. Preliminary trials of a tag for salmon and lobsters. J. Fish. Res. Board Can. 22:421-423.

STASKO, H. B.
1975. Modified lobster traps for catching crabs and keeping lobsters out. J. Fish. Res. Board Can. 32:2515-2520.

STASKO, A. B., T. AMARATUNGA, AND J. F. CADDY.
1977. Northumberland Strait project, Part II. Commercial shellfish data. Can. Fish. Mar. Serv., MS Rep. 1432, 29 p.

TEMPLEMAN, W.
1933. Female lobsters handicapped in growth by spawning. Biol. Board Can., Atl. Coast Stn. Prog. Rep. 6, p. 5-6.
1934. Spring, summer and fall lobster fishing in the southern part of the Gulf of St. Lawrence. Biol. Board Can. Bull. XLIII, p. 13.
1935. Lobster tagging in the Gulf of St. Lawrence. J. Biol. Board Can. 1:269-278.
1936. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime provinces of Canada. J. Biol. Board Can. 2:41-88.

WILDER, D. G.
1947. The lobster fishery of the southern Gulf of St. Lawrence. Fish. Res. Board Can., Atl. Biol. Stn. Circ., Gen. Ser. No. 24, 16 p.
1963. Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20:305-318.
1965. Lobster conservation in Canada. Rapp. P.-v. Réun. Cons. int. Explor. Mer 156:21-29.

WILDER, D. G., AND R. C. MURRAY.
1956. Movements and growth of lobsters in Egmont Bay, P.E.I. Fish. Res. Board Can., Prog. Rep. Atl. Coast Stn. 64, p. 3-9.

AGE, GROWTH, AND DISTRIBUTION OF LARVAL SPOT, *LEIOSTOMUS XANTHURUS*, OFF NORTH CAROLINA

STANLEY M. WARLEN AND ALEXANDER J. CHESTER[1]

ABSTRACT

Age and growth of the early life history stages of spot, *Leiostomus xanthurus*, were determined from daily growth increments on otoliths of larval and early juvenile spot collected from Beaufort Inlet, NC, to the continental shelf break during the fall and winter of 1978-79 and 1979-80. Spawning occurred on the mid to outer continental shelf between early November and early March, but appeared to be concentrated from mid-December through January. Generally, the youngest larvae were found further offshore; ages and lengths increased closer to shore. Larvae entered the estuary at an average age of 59 days (range 40-74 days) and an average size of 13.6 mm (range 11.3-15.6 mm). Significantly younger and smaller larvae immigrated at the beginning and end of the immigration period. Fish entered the estuary segregated by age as indicated by the small within-sample variation in age. A Gompertz growth equation was used to express the relationship between age and standard length for 69 larvae collected in 1978-79 and 557 collected in 1979-80. Spot grew from about 1.6 mm SL at hatching to 17-19 mm SL at 90 days. There were no significant differences in growth parameters between years; age-specific growth rates declined from ≅5%/day at age 10 days to <1%/day at age 90 days.

The larvae of a number of commercially important fishes that spawn on the outer continental shelf of the southeastern United States are transported shoreward to estuaries where development is completed (McHugh 1966; Chao and Musick 1977; Weinstein and Walters 1981; Warlen 1982). Although this general pattern of oceanic spawning and estuarine development has been known at least since publication of the work of Hildebrand and Cable (1930), most recent studies have considered only the estuarine phase (Chao and Musick 1977; Weinstein and Walters 1981), and virtually no quantitative data exist on age and size distribution or growth of larvae between the time of spawning and estuarine immigration.

Spot, *Leiostomus xanthurus*, spawn offshore and are widely distributed in coastal waters from the mid-Atlantic to Texas. Larvae have been reported from North Carolina to Massachusetts (Berrien et al. 1978), from the South Atlantic Bight (Fahay 1975; Powles and Stender 1976), and from the Gulf of Mexico (Fruge 1977; Govoni et al. 1983). Despite studies on egg and larval development (Fruge and Truesdale 1978; Powell and Gordy 1980), growth of juveniles (Weinstein and Walters 1981), and feeding ecology of larvae (Govoni et al. 1983) and juveniles (Chao and Musick 1977), little is known of the early growth history of spot. Our objectives were to 1) determine the estimated age and size distribution of young spot from the time of hatching in the ocean to recruitment into the estuary, 2) estimate larval growth rates, 3) estimate spawning times, and 4) determine when young spot enter the estuary.

METHODS

Sources of Data

Larvae were collected off Beaufort, NC, during 11 2-d cruises of the RV *John de Wolf II*, from December 1978 to April 1979 (grid design, stations 1-10) and from November 1979 to March 1980 (transect design, stations 11-19) (Fig. 1). At all stations, except Beaufort Inlet, samples were obtained from oblique plankton hauls (Powles and Stender 1976) collected with 60 cm diameter bongo nets (mesh sizes 333 or 505 μm) rigged with flow meters. A surface tow was made at Beaufort Inlet. Larvae were also collected with a neuston net (Hettler 1979) about 1 mi inside the mouth of the Newport River at Pivers Island (Fig. 1) seven times from mid-December 1979 to mid-April 1980. Samples were preserved in 95% ethanol (final concentration ≅75%) within 5 min of collection.

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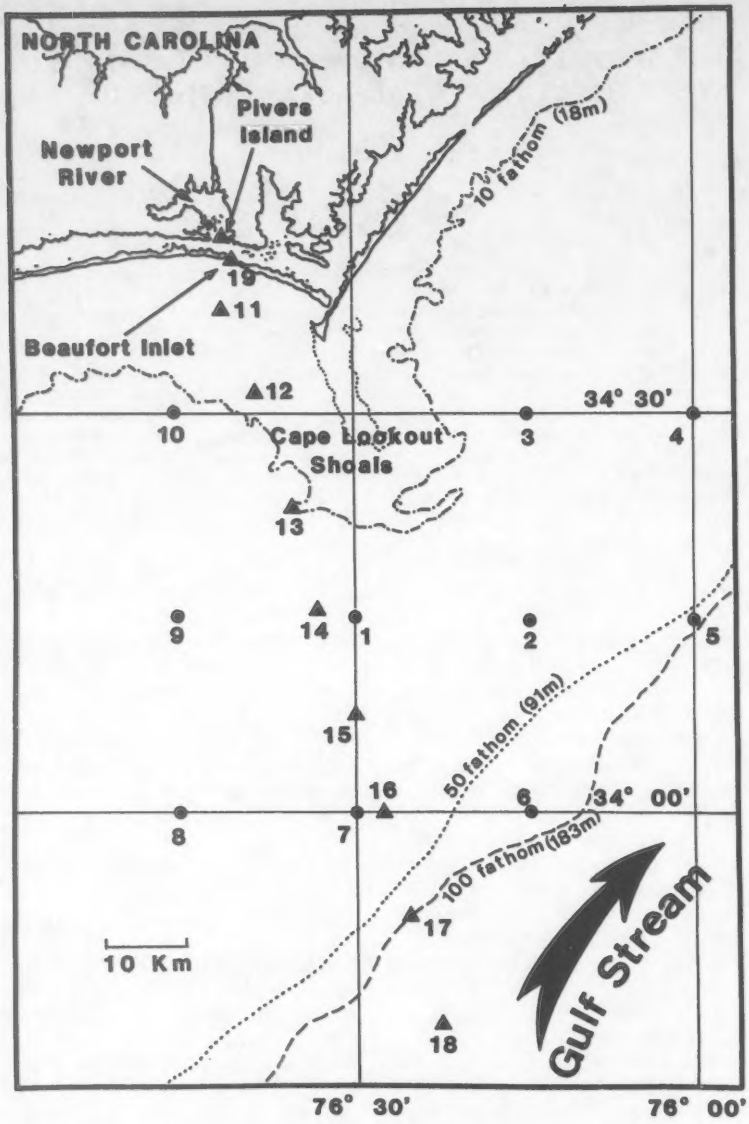

FIGURE 1.—Location of sampling sites for late-larval and early-juvenile spot in the mouth of the Newport River estuary at Pivers Island and for larval spot in the ocean off Beaufort Inlet, NC. Circles are stations sampled from December 1978 to April 1979 and triangles are those sampled October 1979 to April 1980.

Estimated Age and Back-Calculated Length

We counted the number of growth increments on otoliths (e.g., Pannella 1971; Brothers et al. 1976) to estimate age (in days) of each larva. Laboratory-reared larval spot have been shown to deposit an average of 1 ring/d on their otoliths (Peters et al. 1978; Warlen 1984[2]), but do not begin to do so until 5 d after hatching, a time coincident with yolk-sac absorption and first feeding activity at 20°C (Peters et al. 1978). Therefore, we added 5 to the number of counted increments to estimate age. The spawning date of each larva was estimated by subtracting age in days from date of capture.

After we measured each larva in alcohol to the nearest 0.1 mm standard length (SL), we teased the largest pair of otoliths (sagittae) from the surrounding tissue, cleaned them in distilled water, and mounted them on a glass microslide under a thin layer of Flo-Texx[3] mounting medium. They were examined with a compound microscope fitted with a television camera. Growth increments were counted from images of otoliths on a video monitor at magnifications of at least 400×. For selected larvae, otolith radius and the growth increments along it were measured to the nearest 0.1 μm with a filar ocular micrometer. We then used Lee's (1920) modification of the direct proportion formula to back-calculate lengths and reconstruct the growth of each fish. In addition to the assumption that growth increments be daily, the reliability of back-calculated lengths requires that growth of the otolith must be linearly related to growth of the fish. We found, for larvae 2.2-12.4 mm SL, that the relation between body length and otolith radius was linear:

$$\text{body length (mm)} = 2.202 + 0.045 * \text{otolith radius } (\mu\text{m})$$
$$n = 32,\ r^2 = 0.95. \quad (1)$$

Weight-Length Relationships

Because larval fish are not weighed in many ichthyoplankton field studies, a weight-length relationship is required to describe the growth of populations, assess production in terms of dry weight, and estimate weight where only length is known. We determined a dry weight-length relationship from 125 laboratory-reared larvae and early juveniles (2.7-29.6 mm SL). Live fish were anesthetized in a solution of MS-222 (tricane methanesulfonate), removed from the solution, and measured to the nearest 0.1 mm SL. Fish were then rinsed in distilled water, placed on preweighed Nuclepore[R] membrane filters, freeze-dried, and weighed to the nearest 1 μg.

RESULTS

Spawning and Larval Movement

The temporal pattern of spawning found here, though perhaps influenced by the particular dates and stations sampled (Table 1), indicated that spot is a late October-early March spawner (Fig. 2). The majority (67%) of fish collected during the fall and winter of 1979-80 were spawned during December or January (Fig. 2).

The offshore larval distribution by estimated age and length suggests that spawning occurred over the outer continental shelf. Both mean age and length varied inversely with distance from shore (Figs. 3, 4). Youngest (<25 d) and smallest (<4 mm) larvae were found most often near or in the Gulf Stream, 80-100 km off Beaufort Inlet, paralleling the 183 m depth contour (stations 5, 16, 17, 18). However, comparable ages and sizes also were found in the mid-shelf area (stations 1, 14, 15) early in the spawning season (December 1978; November and December 1979). Older (40-50 d) and larger (>8 mm) larvae generally occurred closer to shore within about 40 km of Beaufort Inlet in <25 m of water (stations 10-13, 19), except during February and March 1980 when some larvae were caught 50 km offshore at station 14. Spawning apparently is continuous between late October and late February, since young larvae occurred every month at the three offshore stations (16-18). Most spawning off North Carolina probably occurs between 75 and 95 km offshore, except for some activity in the mid-shelf area early in the spawning season. Our age-length data provided no evidence that spot spawn near shore.

Estuarine Immigration

Larvae entered the Newport River estuary over a 4-mo period from about mid-December to mid-April (Figs. 2, 5). None were caught prior to December 1979 nor after 17 April 1980. Relative abundance of larvae collected at Pivers Island dur-

[2]Warlen, S. M. 1984. Rates of increment formation in otoliths of larval gulf menhaden, *Brevoortia patronus* and spot, *Leiostomus xanthurus*. Unpubl. manuscr. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of larval spot per 100 m^3 caught off North Carolina during the seasons of 1978-79 and 1979-80. N.S. = No sample taken.

1978-79 cruise		Station number									
No.	Date	1	2	3	4	5	6	7	8	9	10
1	6-7 Dec.	1.9	0	0	0	0	0	0	0	0	0
2	4-5 Jan.	5.0	0	N.S.	N.S.	5.6	0	0	19.3	0	0
3	31 Jan.-1 Feb.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0	0
4	7-8 Mar.	1.8	6.4	N.S.	N.S.	N.S.	0	0	1.7	2.7	0
5	26-27 Mar.	0	0	N.S.	N.S.	N.S.	0	0	0	0	13.3
6	23-24 Apr.	0	N.S.	0	0	0	0	0	0	0	0

1979-80 cruise		Station number								
No.	Date	Inlet[1]	11	12	13	14	15	16	17	18
7	15-16 Nov.	N.S.	0	0	0	N.S.	43.1	3.3	N.S.	N.S.
8	3-4 Dec.	N.S.	0	0	3.1	1.1	0	4.0	1.1	45.0
9	15-16 Jan.	N.S.	2.4	0.4	0.7	108.6	8.8	4.1	N.S.	N.S.
10	11-13 Feb.	N.S.	0	0	4.1	31.5	17.9	0.6	0.3	2.3
11	19-20 Mar.	65.6	0	0	0.7	4.2	11.4	0.4	0.6	0

[1]Same as station 19.

ing the winter periods of 1967-70 showed major immigration peaks in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974). The duration of estuarine immigration generally reflected the duration of the spawning season (Fig. 2).

Statistically significant monthly variations (ANOVA, $P < 0.05$) in both age and length of larvae entering the Newport River estuary were observed from December to April (Fig. 5). Mean age at entry increased linearly from December to March and then decreased in April. Thus, larvae spawned at the beginning or end of the season spent relatively less time in the offshore environment than did larvae spawned in the middle of the season. Length followed a similar trend, except during January and early February when it remained about constant, indicating a declining rate of growth. As determined from seven samples collected at Pivers Island (Fig. 5) and one at Beaufort Inlet (19 March 1980), spot entering the estuary averaged 59 d-old (range 40-80).

In general, larvae entering the estuary together had similar spawning dates. As a rule, 50% of the fish in any Pivers Island sample had been spawned within a period of 5 d and all had been spawned within a period of 14 d (Fig. 2). The one exception was the last sample from Pivers Island in which several larvae were more than a month older than the majority of fish. We infer from the generally small variation in age of fish within a sample that a continuum of cohorts moved past Pivers Island enroute to the upstream parts of the estuary and that early juveniles entered the lower estuary segregated by age.

Growth Estimates

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture data for 1978-79 and 1979-80 (Fig. 6). Variance about the estimated growth curve was assumed to represent genetic differences in growth potential and the effects of differing environmental conditions over the year (Pennington 1979). To stabilize the variance of length over the observed age interval, we used the log-transformed version of the Gompertz growth equation:

$$\ln [L_{(t)}] = \ln [L_{(0)}] + \frac{A_{(0)}}{\alpha} [1 - e^{-\alpha t}] \qquad (2)$$

where $L_{(t)}$ = length at time t,
$L_{(0)}$ = length at $t = 0$,
$A_{(0)}$ = specific growth rate at $t = 0$,
α = rate of exponential decay of the specific growth rate.

The time origin ($t = 0$) was selected as hatching time (day 0) and values for $L_{(0)}$, $A_{(0)}$, and α were obtained by nonlinear regression. Age accounted for 96% of the variation in length for one year class (1978-79) and 91% of the variance in length for the other (1979-80) in the log-transformed models. We estimated that spot grew from about 1.6 mm SL at hatching to 17-19 mm at 90 d. The predicted size at hatching agrees well with laboratory observations of Powell and Gordy (1980). Population growth

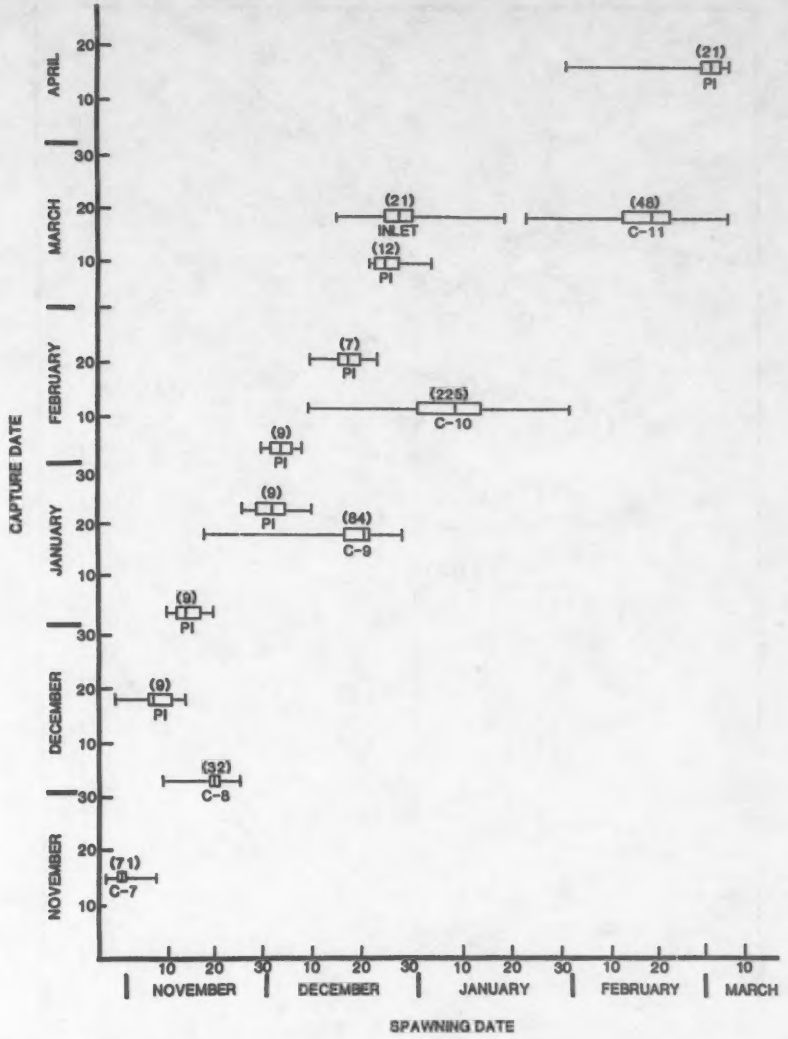

FIGURE 2.—Schematic plots of the spawning times of larval spot caught in the ocean (cruises 7-11 of RV *John de Wolf II*) and late-larvae/early-juvenile spot caught in the Newport River estuary at Pivers Island, NC. In each distribution, the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points.

curves were not significantly different between years [Hotelling's T^2 test of $A_{(0)}$, α, and $L_{(0)}$; Bernard (1981) as modified by Hoenig and Hanumara (1983)]. Age-specific growth rates for both years declined from ≅5%/d at age 10 d to <1%/d at age 90 d.

To determine differences in growth rates for two groups of larvae of different ages but from the same cohort, we back-calculated lengths at 5-d intervals up to 25 d for 10 larvae caught at stations 15 and 16 on 15-16 January 1980 and for 10 larvae caught at Beaufort Inlet on 19 March 1980 (Table 2). Although the estimated mean spawning date for

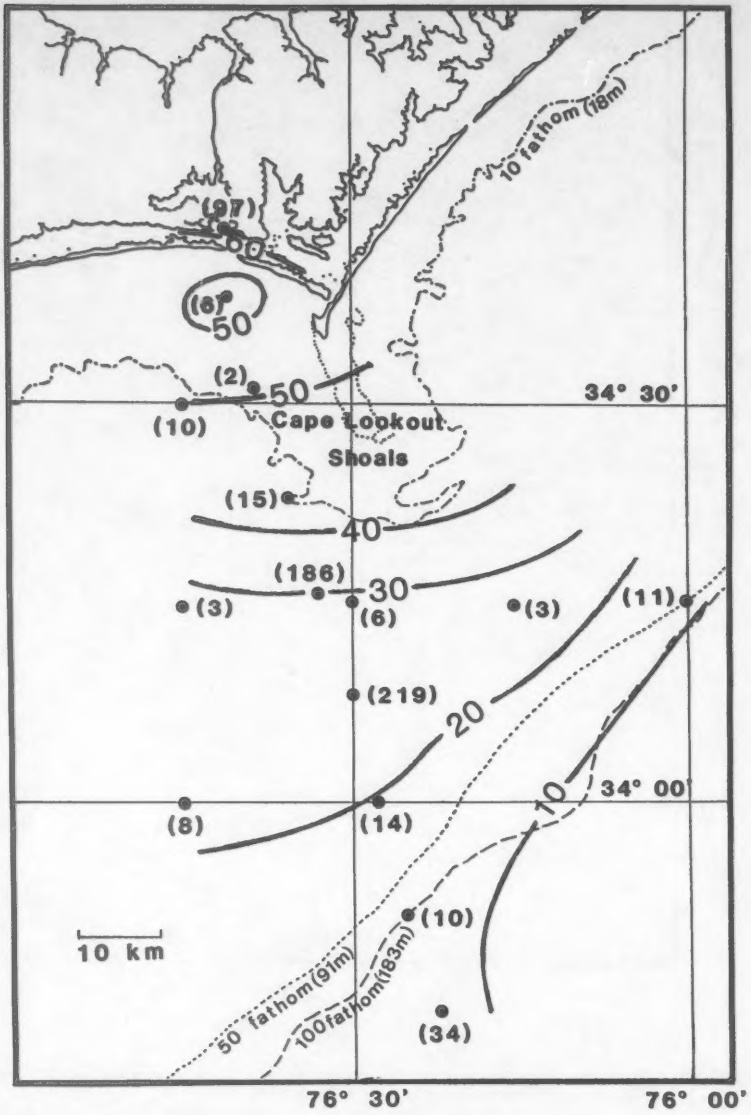

FIGURE 3.—Contour plots of the mean ages of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the numbers of fish aged.

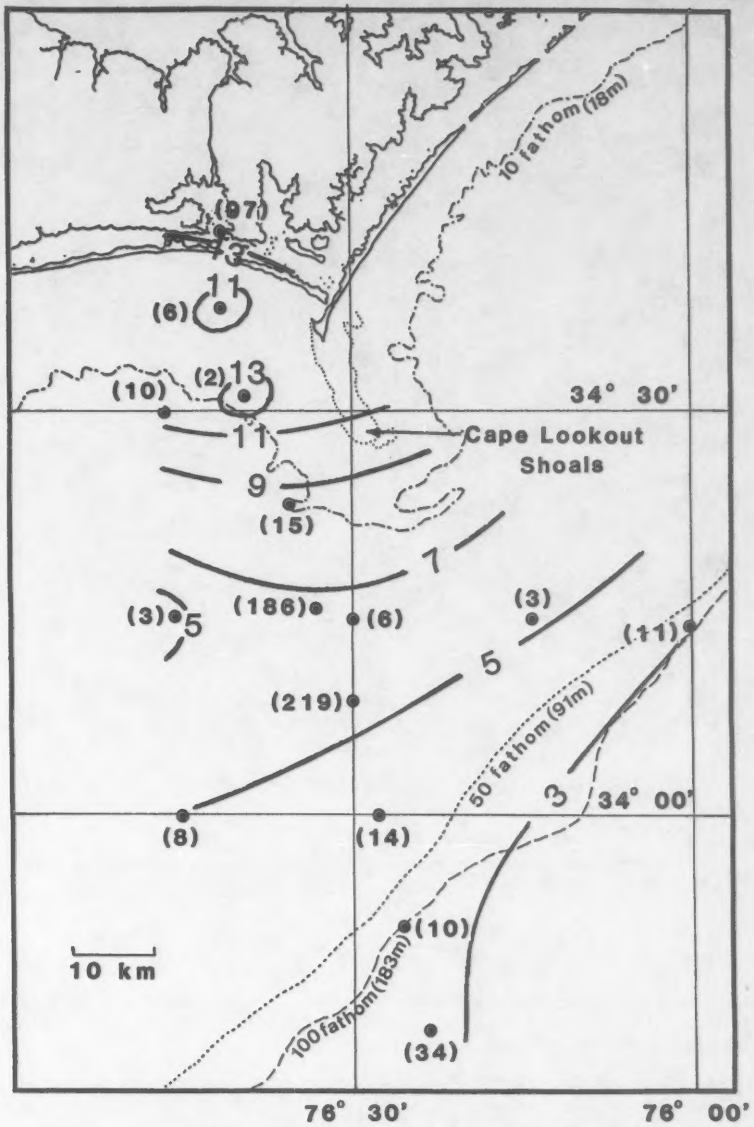

FIGURE 4.—Contour plots of the mean standard length of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the number of fish collected and measured.

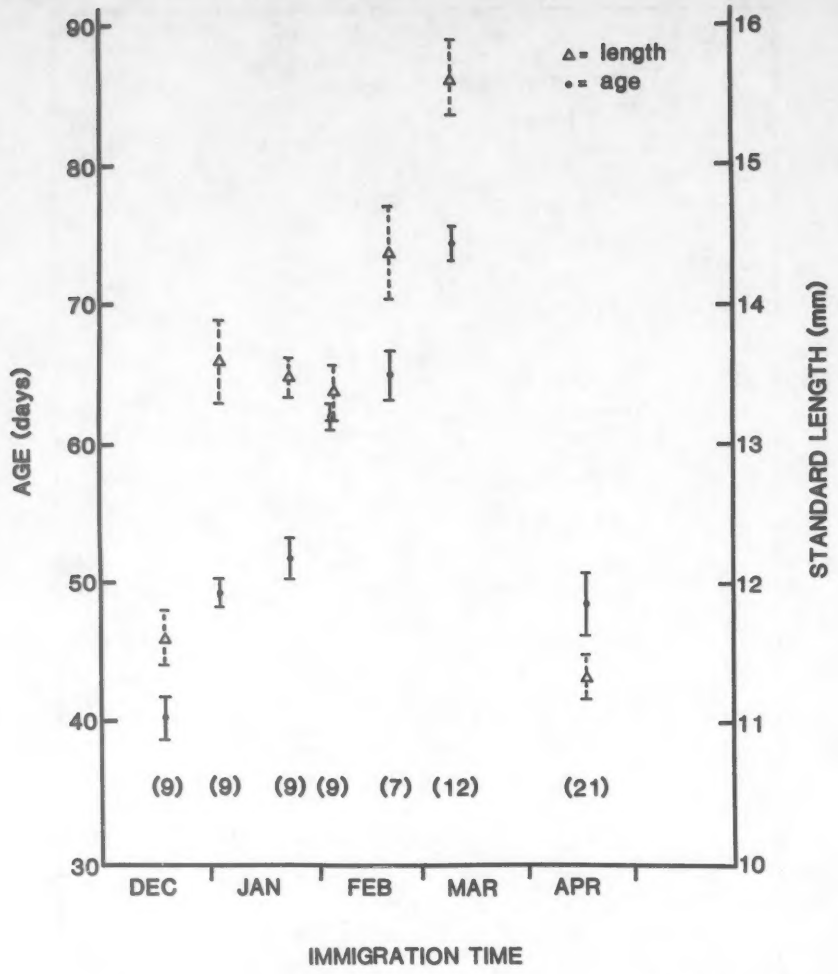

FIGURE 5.—Age (mean ±1 standard error) and standard length (mean ±1 standard error) of late-larval spot entering the Newport River estuary in North Carolina, December 1979-April 1980. The numbers of fish measured and aged at each sampling date are in parentheses.

both groups was identical (22 December 1979), the variance about the mean was greater for Inlet-caught fish. Consequently, back-calculated lengths also were more variable for Inlet-caught fish (F-test, $P < 0.05$), but on the average they appeared to be larger at every age (t-test corrected for unequal variance, $P < 0.05$).

Significant differences were found for the weight-length relation (Fig. 7) of laboratory-reared larvae ≤6 mm and those >6 mm (ANCOVA, $P < 0.001$). We selected 6 mm as the dividing point because basic changes in body form had been observed to occur at around 6 mm (Powell and Gordy 1980). The length exponent for spot ≤6 mm SL (4.201) was close to the mean value (4.152) reported by Laurence (1979) for larvae of seven marine fishes, while larvae > 6 mm (3.282) approached isometric growth (Ricker 1975).

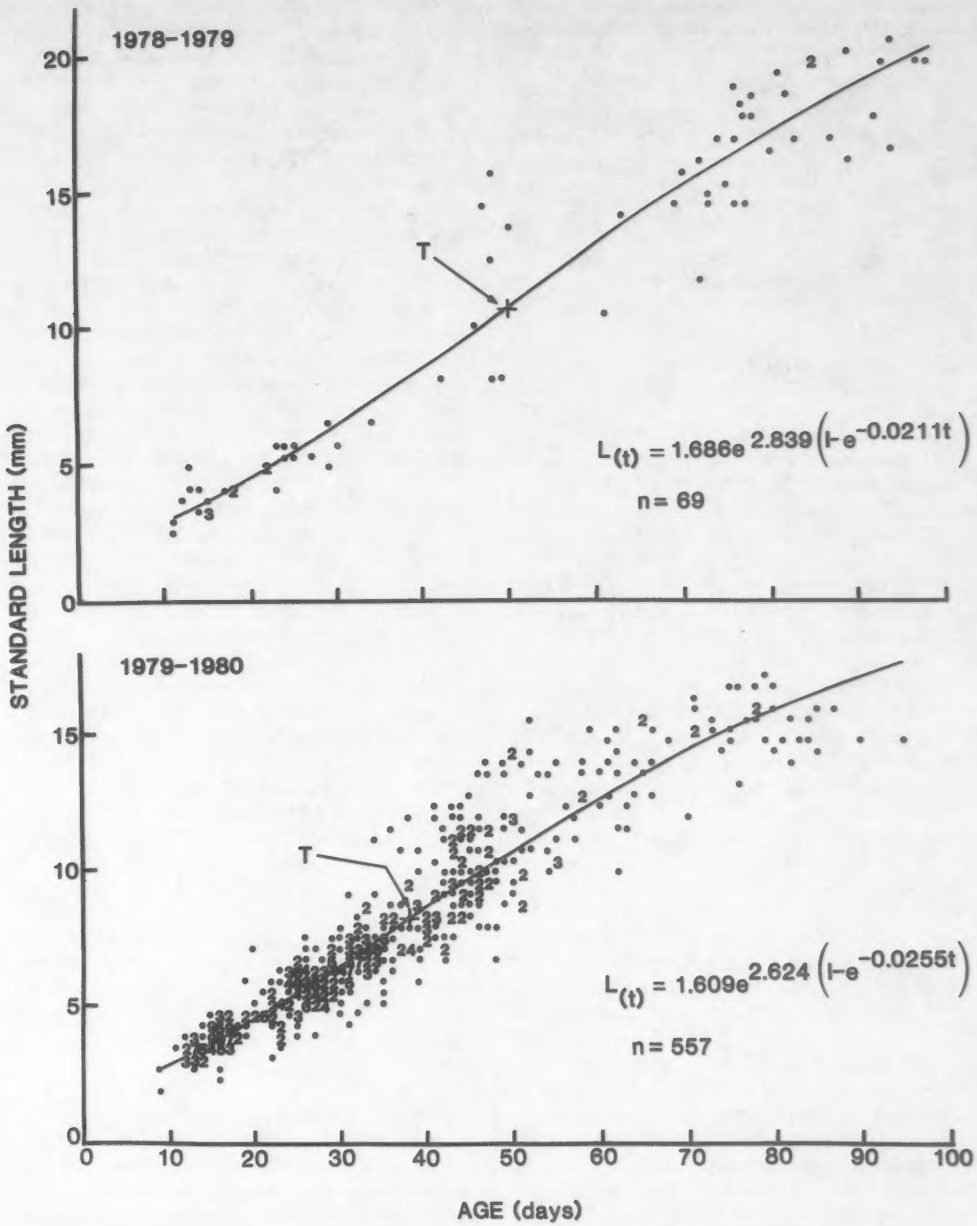

FIGURE 6.—Growth of larval and early-juvenile spot collected from oceanic and estuarine waters of North Carolina in the fall-winter, 1978-79 and 1979-80. The Laird-Gompertz growth model was used to describe the data. Estimates of the parameters were obtained by fitting the log-transformed version of the model to the data. "T" is the point of maximum absolute growth (inflection point) in the growth curve.

TABLE 2.—Mean back-calculated standard length of 10 spot from each of two collections of the same cohort (average spawning date 22 December 1979) taken about 2 mo apart in 1980.

Age (d)	15-16 January Stations 15-16[1] SL (mm)	SD	N	19 March Station 19 (Beaufort Inlet)[2] SL (mm)	SD	N
5	3.1	0.13	10	3.5	0.39	10
10	3.7	0.15	10	4.4	0.49	10
15	4.6	0.32	10	5.1	0.62	10
20	5.1	0.34	7	6.0	0.67	10
25	6.0	0.35	2	7.0	0.80	10

[1]Larval mean age, 23 d; mean size, 5.7 mm
[2]Larval mean age, 83 d; mean size, 15.0 mm

DISCUSSION

Although spot is a winter spawner, it spawns in relatively warm water. Very young larval spot (≤15 d) occurred only in water above 19.3°C, an observation corroborated by experimental evidence indicating that spot spawn only between 17.5° and 25°C (Hettler and Powell 1981). In late fall and early winter off North Carolina, such warm temperatures are found only on the outer continental shelf near the Gulf Stream. Newly ripe adults probably emigrate in the fall of the year from the cooling waters of bays and sounds in Virginia (Hildebrand and Schroeder 1928), North Carolina (Roelofs 1951), and South Carolina (Dawson 1958) to spawn in such warm waters. Hildebrand and Schroeder (1928) and Dawson (1958) also suggested that spot spawn along the outer continental shelf.

Warm coastal waters in the fall and the influence of warm Gulf Stream waters later in the season may provide a suitable spawning temperature regime over a long period. The extended (4.5 mo) spawning season of spot is typical of the general pattern for Atlantic coast sciaenids (Powles 1981). The spawning season of spot in North Carolina in 1979-80 was similar to that found by Hildebrand and Cable (1930) in North Carolina and by Dawson (1958) in South Carolina. Because most of the larvae caught off North Carolina were spawned in December and January, we conclude that these are the months of peak spawning. This conclusion is supported by the observation that peak estuarine immigration occurs in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974) for fish we estimate to have been about 2 mo-old. Hildebrand and Cable (1930) and Lewis and Judy (1983) also inferred, from length-frequency information, that peak spawning occurs in December and January.

The trend of decreasing larval age and size (Figs. 2, 3) with distance from shore supports the idea that spot spend virtually their entire larval period in the ocean. Berrien et al. (1978) and Lewis and Judy (1983) also noted an inverse trend of size with distance from shore in the same area to 79 km offshore. A similar trend may exist in the Gulf of Mexico where Fruge (1977) found small larval spot to be most abundant 60-80 km off the Louisiana coast. By the time larvae have been transported to shore and enter estuarine nursery areas, they have reached the late larval or early juvenile stage.

Although the mechanism is unclear by which larval spot from 74 to 93 km offshore arrive at the estuary in about 60 d, their initial onshore movement is probably a passive transport by water currents in Onslow Bay. A consistent counterclockwise eddy (Stefansson et al. 1971) and a strong indication of bottom drift in a northerly direction on the outer and mid-continental shelf and directly to the coast inshore during January-April (Bumpus 1973) could aid in the transport of larvae. Nelson et al. (1977) considered that zonal Ekman transport was a significant mechanism for movement of larval Atlantic menhaden, *Brevoortia tyrannus*, from offshore spawning grounds to inshore nursery grounds in the same study area at about the same season of year. Data from recent years, however, does not lend support for this hypothesis (Schaaf[4]). A recent analysis by Yoder (1983) suggested that mean Ekman transport does not favor onshore flow in surface waters during winter off the southeastern United States. Rather, cross-shelf transport of larval fishes may depend on highly variable, short-term meteorological events which reverse the mean surface flow. Variations in transport rates of larvae in the ocean as well as spawning at variable distances from shore may be responsible for the seasonal differences in age and length at immigration (Fig. 5). In addition, factors affecting growth, such as temperature and the distribution of food organisms, interact with the physical factors of transport to produce the temporal pattern of age and length observed in a given year.

Young spot undergo several environmentally related changes in growth during their larval and juvenile stages. Growth in length of larval spot is rapid (initially approaching 7%/d) and coincides with the winter peak of plankton productivity in the relatively warm water of the outer continental shelf (Turner et al. 1979; Turner 1981; Yoder et al. 1981;

[4]W. E. Schaaf, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722, pers. commun. January 1984.

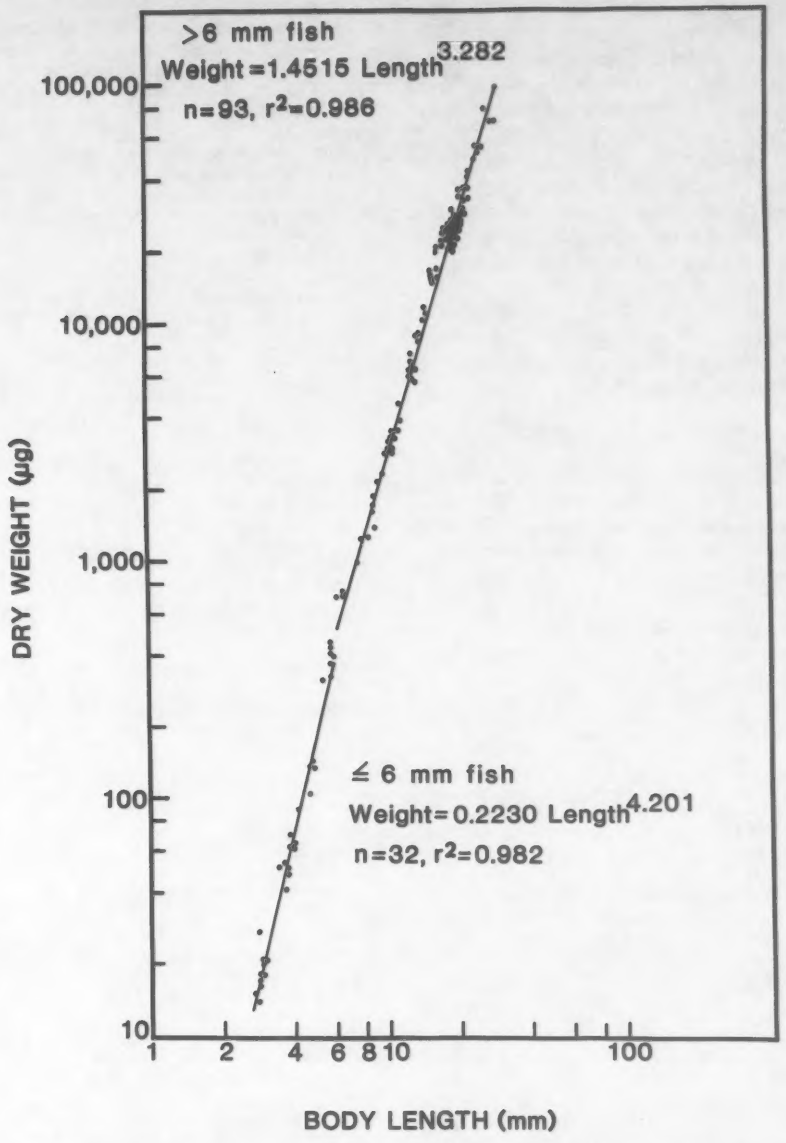

FIGURE 7.—Relationships between dry weight and standard length of spot for length classes ≤6 mm and >6 mm. Fish were from laboratory spawned and reared stocks.

Yoder et al. 1983). By the time larvae enter the cooler (often <10°C) coastal and estuarine waters, growth rate has slowed considerably (<1.5%/d). The asymptote of 22.2 mm SL (Fig. 6, 1979-80 data) estimated by our growth model corresponds closely to the size of juvenile spot collected early in their estuarine residency (Weinstein and Walters 1981). Increase in length of newly immigrated spot is relatively slow (≅0.5%/d from December to March, estimated from figure 3 of Weinstein and Walters 1981), and it is

not until after the usual peak in plankton abundance (Thayer et al. 1974) and increases in water temperature that growth rates accelerate and persist at a high level through the summer (≅1.0%/d from April to August, estimated from figure 3 of Weinstein and Walters 1981).

Within the same cohort, older fish had statistically larger back-calculated sizes at each age than did younger fish (Table 2). One explanation is that size-selective mortality (e.g., predation, Bailey 1984) favors survival of faster growing larvae and that the apparent growth rate depends on the size (and age) of larvae on which it is calculated. Alternatively, the two groups may have been spawned in different locations and experienced different environmental conditions that could affect growth.

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LITERATURE CITED

BAILEY, K. M.
1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Mar. Biol. (Berl.) 79:303-309.

BERNARD, D. R.
1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat. Sci. 38:233-236.

BERRIEN, P. L., M. P. FAHAY, A. W. KENDALL, JR., AND W. G. SMITH.
1978. Ichthyoplankton from the RV *Dolphin* survey of continental shelf waters between Martha's Vineyard, Massachusetts and Cape Lookout, North Carolina, 1965-66. U.S. Dep. Commer., NOAA, Northeast Fish. Cent., Sandy Hook Lab., Tech. Ser. Rep. 15, 152 p.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

BUMPUS, D. F.
1973. A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6:111-157.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

DAWSON, C. E.
1958. A study of the biology and life history of the spot, *Leiostomus xanthurus* Lacépède, with special reference to South Carolina. Contrib. Bears Bluff Lab. 28:1-48.

FAHAY, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the south Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-685, 39 p.

FRUGE, D. J.
1977. Larval development and distribution of *Micropogon undulatus* and *Leiostomus xanthurus* and larval distribution of *Mugil cephalus* and *Bregmaceros atlanticus* off the southeastern Louisiana coast. M.S. Thesis, Louisiana State Univ., Baton Rouge, 75 p.

FRUGE, D. J., AND F. M. TRUESDALE.
1978. Comparative larval development of *Micropogon undulatus* and *Leiostomus xanthurus* (Pisces: Sciaenidae) from the northern Gulf of Mexico. Copeia 1978:643-648.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189-199.

HETTLER, W. F.
1979. Modified neuston net for collecting live larval and juvenile fish. Prog. Fish-Cult. 41:32-33.

HETTLER, W. F., AND A. B. POWELL.
1981. Egg and larval fish production at the NMFS Beaufort Laboratory, Beaufort, N.C., USA. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:501-503.

HILDEBRAND, S. F., AND L. E. CABLE.
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383-488.

HILLDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1-366.

HOENIG, N. A., AND R. C. HANUMARA.
1983. Statistical considerations in fitting seasonal growth models for fishes. Cons. Int. Explor. Mer, C. M. 1983/D:25, 25 p.

LAIRD, A. K., S. A. TYLER, AND A. D. BARTON.
1965. Dynamics of normal growth. Growth 29:233-248.

LAURENCE, G. C.
1979. Larval length-weight relations for seven species of northwest Atlantic fishes reared in the laboratory. Fish. Bull., U.S. 76:890-895.

LEE, R. M.
1920. A review of the methods of age and growth determination of fishes by means of scales. Fish. Invest., Minist. Agric. Fish. Food (G.B.) Ser. II, 4(2):1-32.

LEWIS, R. M., AND M. H. JUDY.
1983. The occurrence of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in Onslow Bay and Newport River estuary, North Carolina. Fish. Bull., U.S. 81:405-412.

MCHUGH, J. L.
1966. Management of estuarine fisheries. *In* R. F. Smith, A. H. Swartz, and W. H. Massman (editors), A symposium on estuarine fisheries, p. 133-154. Am. Fish. Soc., Spec. Publ. 3.

NELSON, W. R., M. C. INGHAM, AND W. E. SCHAAF.
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75:23-41.

PANNELLA, G.
1971. Fish otoliths: Daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

PENNINGTON, M. R.
1979. Fitting a growth curve to field data. *In* J. K. Ord, G. P. Patil, and C. Taillie (editors), Statistical distributions in

ecological work, p. 419-428. Int. Co-op. Publ. House, Fairland, MD.

PETERS, D. S., J. C. DEVANE, JR., M. T. BOYD, L. C. CLEMENTS, AND A. B. POWELL.
1978. Preliminary observations on feeding, growth and energy budget of larval spot (*Leiostomus xanthurus*). *In* Annual Report of the NMFS, Beaufort Laboratory, Beaufort, N.C., to the U.S. Department of Energy, p. 377-397.

POWELL, A. B., AND H. R. GORDY.
1980. Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae). Fish. Bull., U.S. 78:701-714.

POWLES, H.
1981. Eggs and larvae of North American sciaenid fishes. *In* H. Clepper (editor), Marine recreational fisheries 6, p. 99-109. Sport Fish. Inst., Wash., D.C.

POWLES, H., AND B. W. STENDER.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. S.C. Mar. Resour. Cent., Tech. Rep. Ser. 11, 47 p.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

ROELOFS, E. W.
1951. The edible finfishes of North Carolina. *In* H. F. Taylor (editor), Survey of the marine fisheries of North Carolina, p. 109-139. Univ. N.C. Press, Chapel Hill.

STEFÁNSSON, U., L. P. ATKINSON, AND D. F. BUMPUS.
1971. Hydrographic properties and circulation of the North Carolina shelf and slope waters. Deep-Sea Res. 18:383-420.

THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACROIX.
1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15:9-16.

TURNER, R. E.
1981. Plankton productivity and the distribution of fishes on the southeastern U.S. continental shelf. Science (Wash., D.C.) 214:353-354.

TURNER, R. E., S. W. WOO, AND H. R. JITTS.
1979. Estuarine influences on a continental shelf plankton community. Science (Wash., D.C.) 206:218-220.

WARLEN, S. M.
[1982]. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 34:204-214.

WEINSTEIN, M. P., AND M. P. WALTERS.
1981. Growth, survival and production in young-of-year populations of *Leiostomus xanthurus* Lacépède residing in tidal creeks. Estuaries 4:185-197.

YODER, J. A.
1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may affect larval survival. Estuarine Coastal Shelf Sci. 17:637-650.

YODER, J. A., L. P. ATKINSON, J. O. BLANTON, D. R. DEIBEL, D. W. MENZEL, AND G. A. PAFFENHÖFER.
1981. Plankton productivity and the distribution of fishes on the southeastern U.S. Continental Shelf. Science (Wash., D.C.) 214:352-353.

YOKER, J. A., L. P. ATKINSON, S. S. BISHOP, E. E. HOFMANN, AND T. N. LEE.
1983. Effect of upwelling on phytoplankton productivity of the outer southeastern United States continental shelf. Continental Shelf Res. 1:385-404.

ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

DIET OF PACIFIC COD, *GADUS MACROCEPHALUS*, AND PREDATION ON THE NORTHERN PINK SHRIMP, *PANDALUS BOREALIS*, IN PAVLOF BAY, ALASKA

W. D. ALBERS AND P. J. ANDERSON[1]

ABSTRACT

Analysis of 455 Pacific cod, *Gadus macrocephalus*, stomachs collected in 1980 and 1981 from Pavlof Bay, in the western Gulf of Alaska, showed considerable predation on northern pink shimp, *Pandalus borealis*. The most frequently occurring prey items were pink shrimp, *P. borealis*, 63%; euphausids, 41%; walleye pollock, *Theragra chalcogramma*, 27%; and capelin, *Mallotus villosus*, 26%. Pandalid shrimp and snow (Tanner) crab occurred more frequently with increasing cod size (30-69 cm fork length). Euphausids decreased in frequency of occurrence with increasing cod size. Pink shrimp length distributions from cod stomachs and trawl samples were similar. Estimated consumption of pink shrimp by cod in Pavlof Bay ranged from 142 to 857 t over a 112-day period from late May through mid-September 1981. Cod predation may be one reason for the failure of the pink shrimp stock to rebuild in Pavlof Bay following closure of the commercial fishery in 1979. Cod predation may also play a role in keeping other reduced pink shrimp stocks in the western Gulf of Alaska from rebuilding to former levels.

Pacific cod, *Gadus macrocephalus*, predation on northern pink shrimp, *Pandalus borealis*, in Pavlof Bay (Fig. 1) was studied to determine if it is a factor in keeping the pink shrimp stock from rebuilding there. National Marine Fisheries Service (NMFS) and Alaska Department of Fish and Game (ADF&G) survey data from the late 1970's indicate that when pink shrimp populations in regions of western Alaska began to decrease, cod abundance started to increase. Pink shrimp has been reported to be an important food item in the diet of Pacific cod in the Gulf of Alaska (Jewett 1978; Hunter 1979). Predation of pink shrimp by cod may have substantial influence on shrimp stock abundance.

Pavlof Bay was chosen as the study area because it supported a commercial fishery for pandalid shrimp in the 1970's and is suspected to contain a geographically isolated stock of pink shrimp (Anderson 1981). From 1972 through 1979, 13,641 t of pink shrimp were commercially harvested from Pavlof Bay (calculated from ADF&G commercial catch data and NMFS survey data). Survey data from Pavlof Bay indicate that in 1977 and 1978 when pink shrimp abundance began decreasing, cod abundance began increasing (Fig. 2). Following the 1979 season the bay was closed to commercial shrimping due to depressed shrimp abundance levels which remained low through 1983.

This report presents data which suggest that Pacific cod predation is a factor in keeping shrimp stocks from rebuilding. The summer diet of cod, prey size selectivity, and an estimate of pink shrimp biomass consumed by cod in Pavlof Bay during a 112-d period from late May through mid-September 1981 are discussed.

MATERIALS AND METHODS

Pacific cod were collected from 31 tows during three trawl surveys. The first collection was done by NMFS on 25-26 August 1980, the second by ADF&G on 23-25 May 1981, and the third by NMFS on 10-11 September 1981. The collecting was done during daylight hours over a period of about 14 h a day. All three surveys used a high-opening shrimp trawl with an 18.6 m headrope and footrope described by Wathne (1977). Mesh size of the trawl is 32 mm and path-width is about 10 m. Each tow was about 1.8 km in length. Randomly selected sampling locations were restricted to depths >55 m since previous surveys showed that neither shrimp nor cod were found in abundance in shallow water. Both shrimp and cod are uniformly distributed at depths >55 m in Pavlof Bay.

When possible, five stomachs per 5 cm interval of fork length (FL) were removed from every trawl catch and preserved in 10% Formalin[2]. In the

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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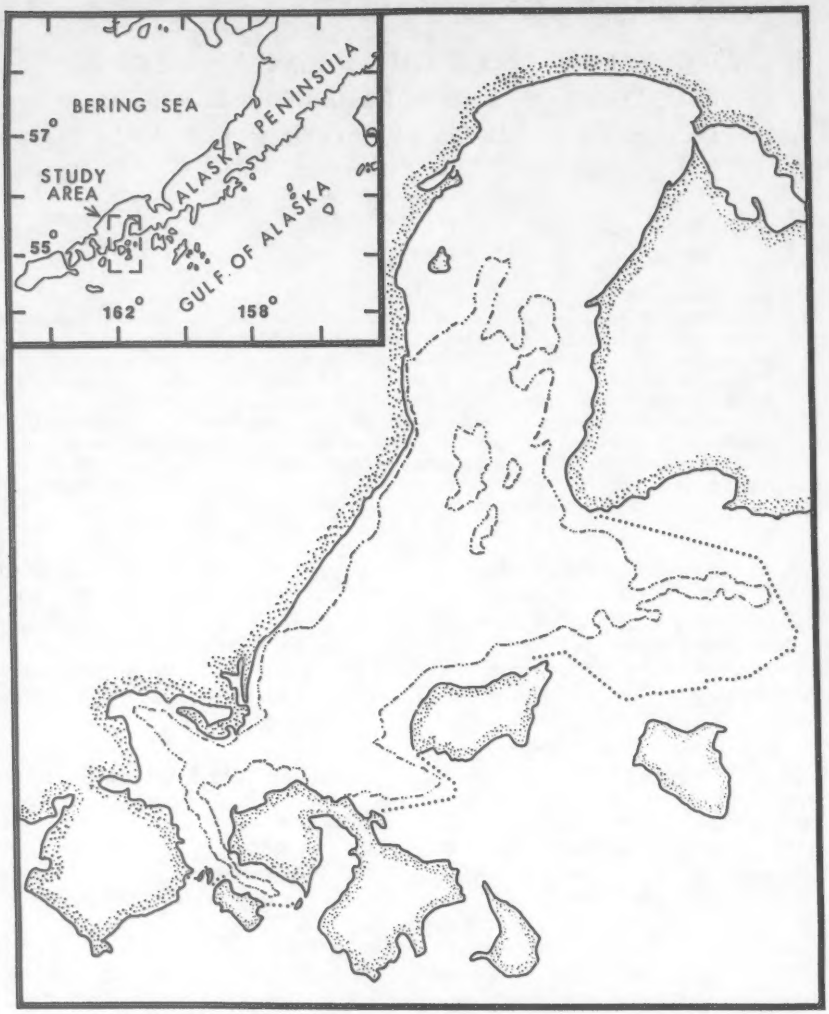


FIGURE 1.—Location of the study area of pink shrimp and Pacific cod (55 m isobath indicated by dotted/dash-line).

laboratory, prey items were sorted to the lowest possible taxon. Frequency of occurrence (number of stomachs containing the food item), number of each prey item, volume by water displacement (nearest 0.1 mL), and wet weight (nearest gram) were recorded. From these measurements, percentages by frequency of occurrence, number, and volume were calculated from non-empty stomachs only.

Size composition was recorded for prey species of commercial importance including pink shrimp (carapace length, CL); humpy shrimp, *Pandalus goniurus*, CL; snow (Tanner) crab, *Chionoecetes bairdi*, carapace width (CW); and walleye pollock, *Theragra chalcogramma*, fork length (FL). Additionally, size composition was recorded for samples of pink shrimp (CL), humpy shrimp (CL), Pacific cod (FL), and walleye pollock (FL) caught in each tow.

To determine if Pacific cod were feeding on selected sizes of pink shrimp, the Kolmogorov-Smirnov test (Sokal and Rohlf 1969) was used to test

for a significant difference between pink shrimp length distributions measured from Pacific cod stomachs and those measured from the trawl. Pink shrimp lengths tested were ≥16.5 mm CL. Anderson (1981) reported that shrimp <16.5 mm CL are not fully vulnerable to trawl capture.

Population biomass estimates for pink shrimp and Pacific cod were calculated using the area swept technique (Alverson and Pereyra 1969).

An estimate of pink shrimp biomass consumed by Pacific cod in Pavlof Bay during the 112-d period between the late May and mid-September 1981 surveys was determined through methods described by Minet and Perodou (1978). Undigested weights (W) of pink shrimp were determined from carapace lengths using the weight-length relationship $W = 0.000802\ (CL)^{2.903}$ (calculated from Pavlof Bay pink shrimp length-weight data). The mean weight of pink shrimp per stomach for each 5 cm length group of Pacific cod was calculated from stomachs where at least 80% of the pink shrimp were measurable (Table 1). A stomach which contained <80% measurable pink shrimp was deemed not suitable for determining the weight of undigested shrimp consumed. These data were then weighted using 768 cod lengths measured during the three surveys. The mean weight of pink shrimp in the stomach of an average-sized cod was then estimated for each survey (Table 1).

The average rates of elimination (r) of food from Pacific cod stomachs collected during the May and September 1981 surveys were calculated from Jones' (1974) equation for food elimination rates from Atlantic gadoids including Atlantic cod, *Gadus morhua*. Jones found that the rates of elimination for the three species of gadoids studied were effectively the same, adjusting for fish and meal size, and temperature. Since Pacific cod are very similar to Atlantic cod, we used Jones' equation in the absence of more relevant information:

$$r\ (\text{g/h}) = \frac{10^{0.035\ (Tb\ -\ Tc)}\ X^{0.46}\ QL^{1.4}}{175}$$

where Tc = 6°C; temperature of the experiment (Jones 1974).

Tb = 5°C (May), 7°C (September); observed temperature in Pavlof Bay from expendable bathythermograph data.

X = 98.9 g (May), 109.0 g (September); the average weight of food found in one stomach. The average weight of food was estimated for each 5 cm length group of Pacific cod and then weighted using 502 cod lengths measured during the May and September surveys. Stomachs containing at least 60% of the greatest weight of food encountered for each cod length group were used to determine X.

Q = 0.12; the average rate of elimination of 1 g of food from the stomach of a 40 cm gadoid (Jones 1974).

L = 52.7 cm (May), 53.0 cm (September); the average length of Pacific cod calculated from 236 fish measured in May and 266 fish measured in September.

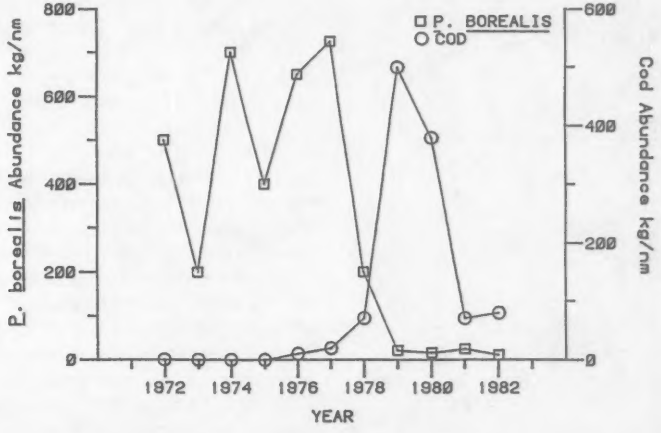


FIGURE 2.—Abundance of pink shrimp and Pacific cod from NMFS summer trawl survey data collected in Pavlof Bay, 1972-82.

TABLE 1.—Calculation of the mean weight of undigested pink shrimp in one stomach for August 1980, May and September 1981.

Length groups of cod (cm)	August 1980			May 1981			September 1981		
	A	B	A×B	A	B	A×B	A	B	A×B
	Number of cod	Mean weight of undigested pink shrimp (g)	Total weight of undigested pink shrimp (g)	Number of cod	Mean weight of undigested pink shrimp (g)	Total weight of undigested pink shrimp (g)	Number of cod	Mean weight of undigested pink shrimp (g)	Total weight of undigested pink shrimp (g)
30-34	2	0	0	—	—	—	—	—	—
35-39	12	0.2	2.4	2	13.6	27.2	3	2.0	6.0
40-44	49	3.5	171.5	9	9.8	88.2	14	3.0	42.0
45-49	137	3.8	520.6	44	19.3	849.2	34	10.1	343.4
50-54	56	7.7	431.2	98	27.2	2,665.6	112	11.3	1,265.6
55-59	9	8.1	72.9	66	17.8	1,174.8	81	12.9	1,044.9
60-64	1	2.5	2.5	14	57.3	802.2	22	12.7	279.4
65-69	—	—	—	3	50.8	152.4	—	—	—
Totals	266		1,201.1	236		5,759.6	266		2,981.3
Mean weight of undigested pink shrimp		1,201.1 / 266 = 4.5 g			5,759.6 / 236 = 24.4 g			2,981.3 / 266 = 11.2 g	

RESULTS

Cod Diet

Of 455 Pacific cod stomachs examined, 435 contained food. Data obtained from cod stomachs collected in August 1980, May 1981, and September 1981 are presented in Table 2. Combining these data, the most frequently occurring prey items were pink shrimp (63%), euphausids (41%), walleye pollock (27%), and capelin, *Mallotus villosus*, (26%). Crustaceans, mostly shrimp, crab, and euphausids, were present in 93% of the stomachs containing food and comprised 45% of the volume. Teleosts, mostly walleye pollock and capelin, were present in 60% of the stomachs containing food and comprised 54% of the volume. Gastropods, bivalves, sipunculids, and ascidians together comprised 1% of the volume.

Crustaceans made up the greatest part of the diet in the May sample and teleosts comprised the greatest part of the diet in the August and September samples (Table 2). Shrimp, mostly pink shrimp, made up 67% of the volume in May compared with 28%, combining August and September data. Crabs, mainly snow crab, comprised 10% of the volume in May compared with 3% in August-September. Teleosts, primarily walleye pollock and capelin, made up 4% of the volume in May and 65% in August-September.

Data on the 10 most frequently occurring food items was categorized by 10 cm length (FL) groups of Pacific cod in a size range of 30 through 69 cm (Table 3). Hurtubia's (1973) trophic diversity method was used to assure that enough stomach samples had been analyzed to give representative values for each length group. Pink shrimp occurred most frequently in all but one length group (30-39 cm) and was the dominant food item by volume in all length groups. Pink shrimp and snow crab increased both in frequency of occurrence and volume with increasing cod size. Conversely, euphausids were the most frequently encountered food item in the 30-39 cm length group, but their frequency of occurrence and volume decreased with increasing cod size. No trends were evident for the occurrence of teleosts. Although data from the three surveys were combined for Table 3, the above trends were evident in each of the surveys.

The size ranges and mean sizes of pink shrimp and humpy shrimp consumed by Pacific cod were similar in general to those found in the trawl (Table 4). Size range and mean size of walleye pollock consumed by cod were considerably smaller than those fish captured by the trawl.

TABLE 2.—Percent frequency of occurrence (*F*), percent by number (*N*), and percent by volume (*V*) of food items in Pacific cod stomachs for August 1980 and May and September 1981. Food categories followed by (total) is the sum of the food items that fall within that category for percent number and percent volume. Percent frequency of occurrence is the number of stomachs containing the food category or item divided by the total number of stomachs containing food.

Food items	August 1980 (*n* = 202)			May 1981 (*n* = 63)			September 1981 (*n* = 170)		
	F	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Crustacea (total)	93.1	92.2	29.4	100.0	99.5	95.0	91.2	57.6	37.6
Amphipoda	—	—	—	—	—	—	1.8	0.3	<0.1
Euphausiacea	53.5	77.0	6.1	81.0	87.3	17.8	12.4	3.3	0.1
Decapoda									
Natantia (total)	71.3	15.0	23.0	76.2	10.4	67.1	80.6	46.1	32.2
Pandalidae	—	—	—	3.2	0.1	0.1	1.8	0.2	<0.1
Pandalus borealis	56.9	9.3	18.5	65.1	7.6	59.7	70.6	34.9	29.9
Pandalopsis dispar	—	—	—	17.5	0.5	1.0	1.2	0.1	<0.1
Pandalus goniurus	20.3	1.7	2.3	25.4	0.4	1.7	4.1	0.9	0.5
Pandalus hypsinotus	0.5	<0.1	0.1	4.8	0.1	1.1	1.2	0.1	0.3
Crangonidae	—	—	—	—	—	—	4.1	0.8	0.2
Crangon sp.	3.0	0.2	0.1	7.9	0.1	0.2	2.9	0.5	<0.1
Crangon communis	2.5	0.2	0.1	12.7	0.2	0.3	18.2	2.9	0.5
Crangon dalli	—	—	—	—	—	—	3.5	0.5	0.1
Argis sp.	—	—	—	4.8	0.1	0.3	1.2	0.1	<0.1
Argis dentata	—	—	—	4.8	0.1	0.3	1.8	0.2	<0.1
Argis lar	—	—	—	—	—	—	4.7	0.7	0.2
Hippolytidae	0.5	<0.1	<0.1	6.3	0.1	0.1	—	—	—
Eualus sp.	0.5	<0.1	<0.1	—	—	—	—	—	—
Eualus macilenta	—	—	—	11.1	0.3	0.2	5.3	0.8	<0.1
Eualus suckleyi	0.5	<0.1	<0.1	1.6	0.1	0.2	2.9	0.4	0.1
Unidentified Natantia	26.7	3.6	1.9	30.2	0.7	1.9	20.0	3.0	0.4
Reptantia (total)	3.5	0.2	0.3	39.7	1.8	10.1	31.2	7.9	5.3
Lithodidae									
Paralithodes camtschatica	0.5	<0.1	<0.1	—	—	—	—	—	—
Majidae									
Chionoecetes bairdi	1.5	0.1	0.2	41.2	1.8	10.0	25.3	6.2	4.7
Paguridae	2.0	0.1	0.1	—	—	—	0.6	0.1	<0.1
Pagurus aleuticus	—	—	—	—	—	—	0.6	0.1	0.2
Pinnotheridae									
Pinnixa sp.	—	—	—	1.6	<0.1	0.1	8.2	1.5	0.4
Osteichthyes (total)	59.4	8.1	68.8	15.9	0.4	3.7	77.1	38.2	60.6
Ammodytes hexapterus	1.5	0.1	0.1	1.6	<0.1	<0.1	—	—	—
Gadus macrocephalus	—	—	—	—	—	—	1.2	0.1	1.8
Hippoglossoides elassodon	0.5	<0.1	1.3	—	—	—	4.7	0.7	4.1
Icelus sp.	—	—	—	—	—	—	0.6	0.1	0.3
Lumpenella longirostris	—	—	—	1.6	<0.1	0.1	—	—	—
Lumpenus sp.	—	—	—	1.6	<0.1	0.1	10.0	1.8	1.3
Lumpenus fabricii	—	—	—	—	—	—	0.6	0.1	<0.1
Lumpenus maculatus	0.5	<0.1	<0.1	—	—	—	—	—	—
Lumpenus sagitta	—	—	—	1.6	<0.1	0.1	—	—	—
Lycodes sp.	—	—	—	—	—	—	0.6	0.1	0.6
Lycodes brevipes	—	—	—	—	—	—	1.2	0.1	0.9
Mallotus villosus	28.7	4.6	32.7	4.8	0.1	1.4	29.4	8.9	20.5
Theragra chalcogramma	13.4	.7	24.8	1.6	<0.1	1.2	51.8	17.0	21.9
Trichodon trichodon	—	—	—	—	—	—	5.9	0.7	4.3
Zaprora silenus	—	—	—	—	—	—	0.6	0.1	0.7
Unidentified Osteichthyes	30.7	2.7	9.9	14.3	0.3	0.8	37.1	8.5	4.2
Bivalvia (total)	1.0	0.1	0.1	4.8	0.1	0.1	14.7	3.1	0.1
Clinocardium sp.	0.5	<0.1	<0.1	3.2	<0.1	<0.1	1.8	0.2	<0.1
Macoma sp.	—	—	—	—	—	—	0.6	0.1	<0.1
Yoldia sp.	—	—	—	3.2	<0.1	<0.1	12.4	2.6	<0.1
Unidentified Bivalvia	0.5	<0.1	<0.1	1.6	<0.1	<0.1	1.8	0.2	<0.1
Gastropoda (total)	1.0	0.1	0.1	3.2	0.1	0.1	0.6	0.1	<0.1
Naticidae	1.5	0.1	0.1	1.6	<0.1	<0.1	—	—	—
Neptunidae	—	—	—	1.6	<0.1	<0.1	0.6	0.1	<0.1
Trochidae									
Margarites sp.	—	—	—	1.6	<0.1	<0.1	—	—	—
Unidentified Gastropoda	—	—	—	1.6	<0.1	<0.1	—	—	—
Ascidiacea	0.5	<0.1	0.2	—	—	—	—	—	—
Sipuncula (Phylum)	0.1	<0.1	0.1	1.6	<0.1	0.1	2.4	0.4	0.6
Plant	2.0	0.1	1.4	3.2	<0.1	0.9	4.7	0.6	1.0
Pebbles	2.5	—	0.1	19.0	—	0.4	18.8	—	0.4

TABLE 3.—The 10 most frequently occurring food items are categorized by 10 cm length (FL) groups of Pacific cod from 30 to 69 cm. Data is presented by percent frequency of occurrence (*F*), percent by number (*N*), and percent by volume (*V*).

	30-39 cm (*n* = 20)			40-49 cm (*n* = 216)			50-59 cm (*n* = 173)			60-69 cm (*n* = 23)		
Food items	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Euphausiacea	78.8	51.3	7.5	54.7	58.3	9.0	48.1	54.8	8.9	27.3	32.7	3.0
Pandalus borealis	36.4	15.1	31.9	61.0	19.0	30.6	69.9	17.7	36.4	81.8	29.7	47.6
Pandalus goniurus	3.0	0.5	0.9	13.8	0.7	1.2	20.2	1.3	1.2	22.8	0.6	0.9
Crangon sp.	5.6	2.4	<0.1	3.5	0.2	0.1	4.0	0.3	0.1	9.0	0.3	0.2
Crangon communis	—	—	—	10.1	0.9	0.4	12.9	1.2	0.3	18.2	1.4	0.5
Eualus macilenta	11.1	0.3	0.3	5.2	0.3	0.1	6.7	0.4	0.1	—	—	—
Chionoecetes bairdi	—	—	—	11.5	1.4	2.5	26.7	3.0	5.1	59.1	5.3	9.0
Lumpenus sp.	—	—	—	4.3	0.9	0.8	3.5	0.5	0.4	4.5	0.2	0.3
Mallotus villosus	14.1	8.7	28.3	19.6	3.5	18.3	24.4	4.7	17.5	22.8	4.7	9.3
Theragra chalcogramma	16.7	9.5	8.5	20.5	4.4	15.2	22.7	6.3	16.7	13.7	6.3	3.9

All sizes of cod examined were feeding on both small and large pink shrimp. Pink shrimp length (CL) distributions measured from cod stomachs and from trawl samples began to overlap at about 12 mm (Fig. 3). Results from the Kolmogorov-Smirnov test comparing pink shrimp length distributions ≥16.5 mm CL from cod stomachs and trawl samples showed no significant difference ($P > 0.10$) in August 1980 and May 1981. There was a significant difference ($P = 0.009$) in the September 1981 sample. No significant difference between length distributions indicates that cod were not feeding on selective sizes of pink shrimp. A significant difference indicates that cod consumed a greater proportion of smaller shrimp than was captured by the trawl.

stomach were 24.4 g for May and 11.2 g for September 1981 (Table 1). Per day, the average amount of pink shrimp consumed by one cod was 8.1 g and 3.7 g for May and September, respectively. The estimated weight of an average length cod was 1,689.5 g for the May survey and 1,720.1 g for the September survey ($W = 0.00000593L^{3.168}$; Owen and Blackburn 1983). Cod biomass estimates were 1,621 t for May and 591 t September, respectively.

Based on the above parameters, estimates of pink shrimp biomass consumed were calculated using the May and September data (Table 5). With May data, Pacific cod consumed an estimated 875 t of pink shrimp over the 112-d period, whereas the

TABLE 4.—Size range and mean size of prey and trawl caught animals. Size data were not collected for snow crab in the trawl. CL = carapace length; FL = fork length; CW = carapace width.

	Number measured		Size range		Mean size	
	Prey	Trawl	Prey	Trawl	Prey	Trawl
Pink shrimp	1,143	7,823	6.5-26.0 mm (CL)	10.0-26.0 mm (CL)	16.2 mm	18.0 mm
Humpy shrimp	102	202	8.0-17.5 mm (CL)	10.5-18.5 mm (CL)	13.5 mm	13.9 mm
Walleye pollock	236	2,100	6.0-25.0 cm (FL)	6.0-63.0 cm (FL)	10.3 cm	22.8 cm
Snow crab	69	—	6.0-42.0 mm (CW)	—	22.2 mm	—

Estimate of Pink Shrimp Biomass Consumed

The extent of the Pacific cod predation on pink shrimp in Pavlof Bay was examined by estimating total biomass consumed during a 112-d period from late May through mid-September 1981. Analysis using Jones' (1974) equation indicated that for both 1981 surveys the average amount of food found in a cod stomach was digested in about 3 d. The average weights of undigested pink shrimp found in a cod

TABLE 5.—Calculation of the total pink shrimp biomass consumed by Pacific cod during a 112-d period from late May through mid-September 1981. Two estimates are presented using the May and September data.

	May 1981	Sept. 1981
Mean weight of pink shrimp consumed daily by one cod (g)	8.1	3.7
112-d consumption by one cod (g)	907.2	414.4
Weight of an average length cod (g)	1,689.5	1,720.1
Proportion of pink shrimp eaten relative to cod weight	0.54	0.24
Cod biomass estimate (t)	1,621	591
Pink shrimp biomass consumed (t)	875	142

September information suggests that cod consumed an estimated 142 t of pink shrimp over the same period.

DISCUSSION

Cod Diet

Pink shrimp was the dominant food item identified by frequency of occurrence (63%) and percent volume (31%). In the Gulf of Alaska near Kodiak Island, Jewett (1978) reported pink shrimp occurring in 4% of the Pacific cod examined, and Hunter (1979) found pink shrimp occurring in 24% of the cod, representing 16% of the diet by weight. Hunter also identified pink shrimp as the dominant food item in his study. However, our study exhibited a higher percent frequency of occurrence for that species. Unlike our study, Jewett and Hunter's studies included examinations of cod from offshore areas, which were not regions of high pink shrimp density (Gaffney 1977[3]).

The prey size ranges of walleye pollock and snow crab in our study were similar to those found by Hunter (1979). In our study, the maximum length of walleye pollock consumed by cod was 25 cm FL, although the majority were between 6 and 20 cm. Hunter (1979) reported that cod around Kodiak Island were feeding on groundfish (including walleye pollock) between 2 and 24 cm. The snow crab consumed by cod in Pavlof Bay ranged from 5 to 45 mm CW, which is similar to the size range of snow crab (1-40 mm) found in cod stomachs by Hunter (1979). Jewett (1978) reported a greater size range of snow crab occurring in cod stomachs (from 1.8 to 70 mm), yet 78% were between 7 and 23 mm. The maximum size of cod examined by Jewett was 92 cm TL (total length) compared with 69 cm FL in our study, and this difference probably accounts for his observation of larger snow crab.

We believe that cod were not feeding on selected sizes of shrimp. The size ranges and mean sizes of pink shrimp and humpy shrimp consumed by cod were similar to those found in the trawl (Table 4). However, cod did consume small (<10.0 mm CL) pink shrimp that were not captured by the trawl. We believe this is due to trawl bias toward larger shrimp. No significant difference was found between pink shrimp length distributions from cod stomachs and trawl samples in two of the three surveys, indicating that cod were not feeding on selected sizes of shrimp. There was a significant difference ($P = 0.009$) for the September 1981 survey. In this sample either cod selected slightly for smaller shrimp or the trawl caught slightly larger shrimp.

Estimate of Pink Shrimp Biomass Consumed

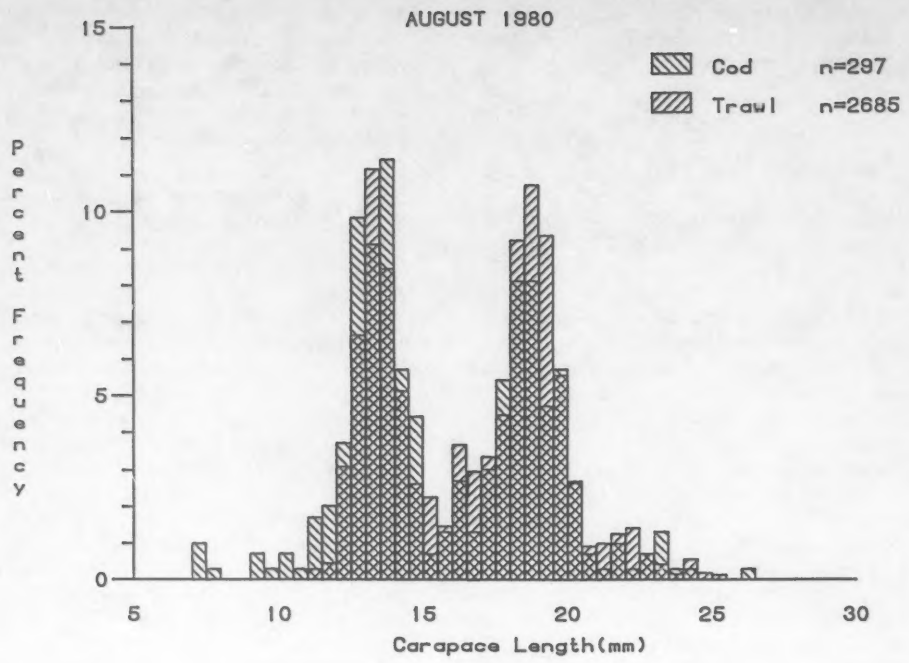
The estimated pink shrimp biomass in Pavlof Bay decreased by 1,501 t between the May and September surveys in 1981. During this period we estimated that Pacific cod consumed between 142 and 875 t of pink shrimp. Since Pavlof Bay is believed to contain a geographically isolated stock of pink shrimp (Anderson 1981) and because the bay was closed to shrimp fishing in 1981, cod predation is responsible for at least part of the biomass decline.

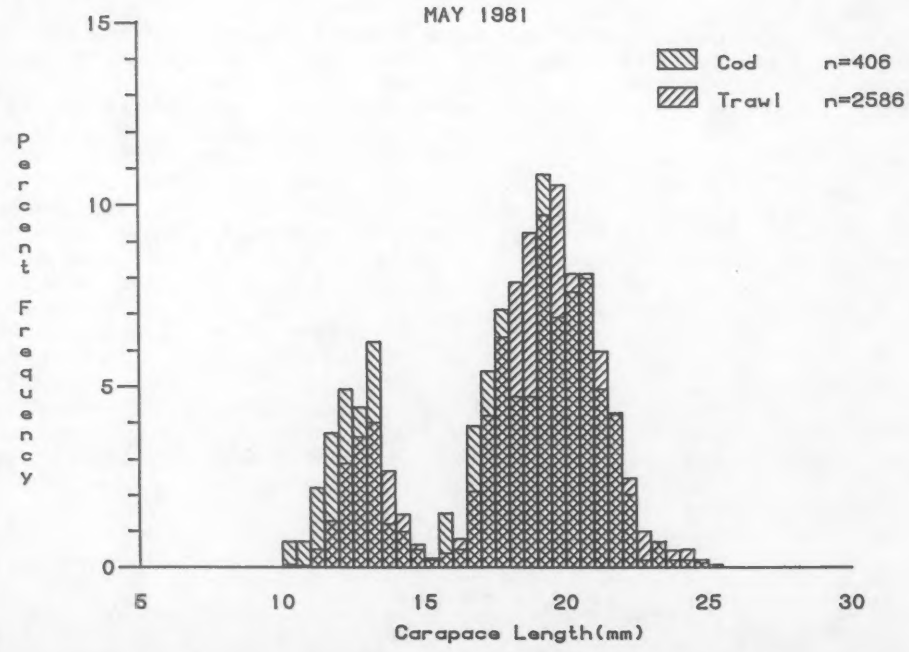
The estimate of pink shrimp biomass consumed over the 112-d period using the May survey data was 733 t more than was estimated using September data. Two of the parameters used to calculate consumption estimates were responsible for this difference. In May the mean weight of pink shrimp consumed daily by one cod was about double the amount in September. Pink shrimp were more abundant and made up a larger percentage of the diet in May than in September. Additionally, cod biomass was estimated to be almost three times higher in May than it was in September causing the consumption estimate to be higher in May (Table 5).

We belive that consumption of pink shrimp by cod probably lies toward the high end of the calculated range (142-875 t). Biomass estimates were probably conservative for pink shrimp and Pacific cod. Biomass was calculated on the assumption that all cod and shrimp were on bottom and all those in the path of the trawl were caught. This is not true for cod or shrimp. For example, Edwards (1968) reported that up to 49% of the gadoids in the path of a trawl avoid capture. Also, an estimate of the catchability of shrimp with the high-opening shrimp trawl was about 56% (Alaska Department of Fish and Game 1982[4]). If the cod biomass estimate was conservative, the consumption of pink shrimp by cod would be higher than calculated. Further, if the pink shrimp biomass estimate was conservative, the calculated

[3]Gaffney, F. G. 1977. Kodiak pandalid shrimp research. Commercial Fisheries Research and Development Act, Project No. 5-36-R. Unpubl. manuscr., 76 p. National Marine Fisheries Service, NOAA, Wash., DC 20235.

[4]Westward Region Shellfish Staff, Alaska Department of Fish and Game. 1982. Westward Region Shrimp Fishery Management Plan. Unpubl. manuscr., 70 p. Alaska Department of Fish and Game, Kasheruaroff, Mission Road, P.O. Box 686, Kodiak, AK 99615.


AUGUST 1980
Cod n=297
Trawl n=2685
Percent Frequency
15
10
5
0
5
10
15
20
25
30
Carapace Length(mm)


MAY 1981
Cod n=406
Trawl n=2586
Percent Frequency
15
10
5
0
5
10
15
20
25
30
Carapace Length(mm)

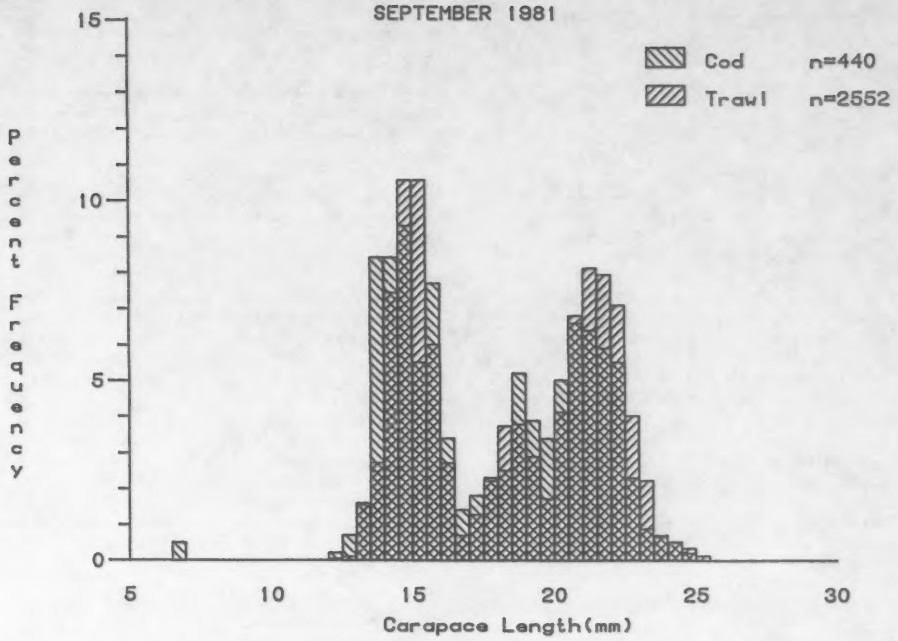


FIGURE 3.—Size distribution of pink shrimp from trawl samples and Pacific cod stomachs for August 1980 and May and September 1981.

biomass decline of pink shrimp between May and September 1981 would also be greater.

Pacific cod are probably feeding on pink shrimp in Pavlof Bay the entire year although the largest concentrations of cod are likely to occur from spring through fall. Trawl survey data from Pavlof Bay indicate that cod biomass decreased from 93 t in September 1978 to 20 t in February 1979 and then increased to 371 t in May 1979. Pacific cod are migratory; they move to shallow areas (<90 m) in spring to feed and return to deeper areas (165-247 m) offshore in fall or winter to spawn (Moiseev 1953). The majority of Pavlof Bay is <90 m deep which is not preferred winter habitat.

Although we believe that Pacific cod predation has an effect on the present reduced population of pink shrimp, predation probably was not the primary reason for the initial decline of pink shrimp in Pavlof Bay that began in 1977. At that time Pacific cod abundance was just beginning to increase (Fig. 2). Fishing removed about 3,819 t (calculated from ADF&G commercial catch data and NMFS survey data) of pink shrimp between the 1977 and 1978 surveys, which was 30% of the estimated available biomass in 1977. This harvest and the dying out of the strong 1971 year class (Anderson 1981) were probably responsible for most of that initial decrease. Cod predation did become a factor, however, once the pink shrimp resource was reduced. This impact on pink shrimp appears substantial despite the reduction of cod in Pavlof Bay (Fig. 2).

ADF&G (footnote 4) has reported diminishing pink shrimp stocks in other areas of the western Gulf of Alaska. Some areas that once contained high concentrations of pink shrimp experienced reductions in abundance at the same time as Pavlof Bay. In most areas, no increase in pink shrimp abundance was observed through 1982, though many areas were closed to fishing. Like Pavlof Bay, these other areas experienced an increase in Pacific cod abundance about the same time as pink shrimp populations were declining. Cod predation may play a role in keeping these reduced pink shrimp stocks from rebuilding to former levels.

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LITERATURE CITED

ALVERSON, D. L., AND W. T. PEREYRA.
1969. Demersal fish explorations in the northeastern Pacific Ocean - an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26:1985-2001.

ANDERSON, P. J.
1981. A technique for estimating growth and total mortality for a population of pink shrimp *Pandalus borealis* from the western Gulf of Alaska. *In* T. Frady (editor), Proceedings of the International Pandalid Shrimp Symposium, February 13-15, 1979, Kodiak, Alaska, p. 331-342. Univ. Alaska, Fairbanks, AK, Sea Grant Program, Sea Grant Rep. 81-3.

EDWARDS, R. L.
1968. Fishery resources of the North Atlantic area. *In* D. W. Gilbert (editor), The future of the fishing industry of the United States, p. 52-60. Univ. Wash. Publ. Fish., New Ser. 4.

HUNTER, M. A.
1979. Food resource partitioning among demersal fishes in the vicinity of Kodiak Island, Alaska. M.S. Thesis, Univ. Washington, Seattle, 120 p.

HURTUBIA, J.
1973. Trophic diversity measurement in sympatric predatory species. Ecology 54:885-890.

JEWETT, S. C.
1978. Summer food of the Pacific cod, *Gadus macrocephalus*, near Kodiak Island, Alaska. Fish. Bull., U.S. 76:700-706.

JONES, R.
1974. The rate of elimination of food from the stomachs of haddock, *Melanogrammus aeglefinus*, cod *Gadus morhua* and whiting *Merlangius merlangus*. J. Cons. Int. Explor. Mer 35:225-243.

MINET, J. P., AND J. B. PERODOU.
1978. Predation of cod, *Gadus morhua*, on capelin, *Mallotus villosus*, off eastern Newfoundland and in the Gulf of St. Lawrence. Int. Comm. Northwest Atl. Fish. Res. Bull. 13: 11-20.

MOISEEV, P. A.
1953. Treska i kambaly dalnevostochnykh morei (Cod and flounders of far-eastern seas). [In Russ.] Izv. Tikhookean. Nauchno-Issled Inst. Rybn. Khoz. Okeanogr. 40:1-287. [Engl. transl. by Fish. Res. Board Can., Transl. Ser. No. 119, 576 p.]

OWEN, D. L., AND J. E. BLACKBURN.
1983. Bottomfish catch and trawl data from an otter trawl survey in northern Shelikof Strait, Chignik area, and Chiniak gully, Alaska, July and August 1981. Alaska Dep. Fish Game, Tech. Data Rep. 82, 68 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, 776 p.

WATHNE, F.
1977. Performance of trawls used in resource assessment. Mar. Fish. Rev. 39(6):16-23.

VERTICAL DISTRIBUTION OF ICHTHYOPLANKTON OFF THE OREGON COAST IN SPRING AND SUMMER MONTHS

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ABSTRACT

Day and night discrete-depth tows were taken off the Oregon coast in spring and summer months to assess the vertical distribution of ichthyoplankton in nearshore waters. Over 1,000 larvae representing 33 taxa of both coastal and offshore ichthyoplankton assemblages were taken; *Psettichthys melanostictus* was the most abundant coastal species and *Lyopsetta exilis* the most abundant offshore species. Larvae were generally most abundant at 10-30 m, near the seasonal thermocline in both day and night collections. Larval abundance in July was much higher than in April-May collections. Limited evidence for diel vertical migration suggests that *Psettichthys melanostictus* moves to surface waters at night and *Gadus macrocephalus* moves to deeper water at night. No trends of changes in depth distribution were observed with increasing size.

Knowledge of the vertical distributions of larval fishes is crucial to full understanding of their biology and to understanding the results of ichthyoplankton surveys (Ahlstrom 1959; Kendall and Naplin 1981). The interaction between vertical distributions and physical processes can have important effects on onshore-offshore distributions of planktonic organisms in upwelling regions such as the coastal northeastern Pacific (Peterson et al. 1979; Parrish et al. 1981; Wroblewski 1982; Rothlisberg et al. 1983). Near-surface distribution, for example, may result in shoreward transport in slicks associated with internal waves (Shanks 1983). In the coastal region off Oregon, the only information on larval fish vertical distribution is a comparison between abundances of *Parophrys vetulus* and *Isopsetta isolepis* larvae from neuston and oblique bongo net tows (Laroche and Richardson 1979) and one 24-h study with stratified samples taken by bongo nets without opening-closing devices (Richardson and Pearcy 1977). With the exceptions of the classic study by Ahlstrom (1959) and recent studies by Brewer et al. (1981) and Schlotterbeck and Connally (1982), little else is known about the vertical distribution of larval fishes in northeastern Pacific coastal waters. In this paper, we present information on vertical distributions of larval fishes off Oregon.

METHODS

Six series of samples were collected in 1982, four during daylight (30 April, 14 May, 2 and 13 July) and two during night (2 and 6-7 July). The first two series (30 April, 14 May) were taken at station NH10, 10 nmi (18.5 km) off Newport, OR, on the Newport hydroline (lat. 44°40'N; Fig. 1). All others were collected at NH5 (9.2 km offshore). Each sample series consisted of a variable number of tows at discrete depth strata from the surface to within about 4 m of the bottom (Table 1).

Tows were stepped oblique in five intervals of 3 min each, resulting in a total sampling time of 15 min in each 5 or 10 m depth stratum. The sampler was an opening-closing Tucker trawl (Clarke 1969) with three nets and a double-release mechanism operated by messengers. The nets were 0.505 mm mesh (Nitex[3]) with a 1 m^2 mouth; all tows were at a wire angle of 45° at approximate tow speeds from 0.9 to 1.1 m/s. At this angle, effective mouth area of the net is 0.71 m^2. An uncontaminated, discrete depth sample was collected in the second net by lowering the trawl with the first net open, opening the second net for the desired sampling time, and retrieving the trawl with the third net open. Water volumes filtered were estimated with General Oceanics flowmeters mounted in the center of each net. Volumes of water filtered usually ranged between 250 and 450 m^3/sample. Temperature and salinity data were collected throughout the water column on each cruise using Niskin bottles to collect

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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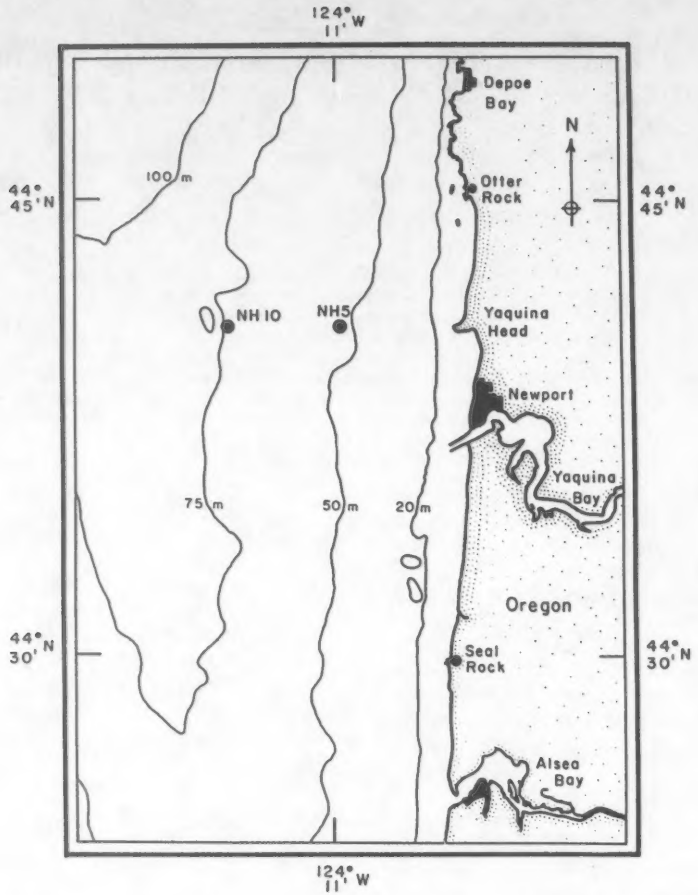

FIGURE 1.—Locations of the sampling conducted during the present study. NH5 and NH10 indicate the stations used.

TABLE 1.—Number of tows per depth stratum with total volumes filtered. (Asterisk indicates that for subsequent analysis the NH10 day sample in the two deepest categories were combined with the 50-60 m stratum.) Sample times were as follows: Day—4/30, 1018-1547; 5/14, 0808-1600; 7/2, 0608-0907; 7/13, 0554-1048; night—7/2, 0016-0514, 7/6-7/7, 2330-0410.

	Day						Night		
	NH10			NH5			NH5		
Depth (m)	4/30	5/14	Total volume filtered (m^3)	7/2	7/13	Total volume filtered (m^3)	7/2	7/6-7/7	Total volume filtered (m^3)
0-5	2	2	1,682.7	2	2	1,392.6	2	2	1,574.8
5-10	2	2	1,783.7	2	2	1,451.2	2	2	1,575.7
10-20	2	2	1,595.7	1	2	862.9	2	2	1,292.9
20-30	2	2	1,796.7	1	2	929.3	2	2	1,237.6
30-40	1	2	1,415.8	1	2	920.5	1	2	1,184.0
40-50	1	2	1,488.1	1	2	920.9	1	2	1,034.8
50-60	1	2	1,891.2	1	2	671.3	1	1	808.3
60-70*	1	1	930.0	—	—	—	—	—	—
70-80*	—	1	704.8	—	—	—	—	—	—

water samples at 5 to 10 m intervals or using a self-contained Applied Microsystems CTD-12. The salinities of water bottle samples were determined in the laboratory using a Guideline 8400 autosalinometer. The CTD salinities from 13 July were not used because of suspected machine malfunction. The CTD temperatures from 13 July agreed with surface bucket temperatures and were used in our study.

Plankton samples were preserved at sea in 10% buffered Formalin. Samples were sorted for fish larvae in the laboratory using a dissecting microscope. Larvae were identified to the lowest possible taxon, measured (standard length), and stored in 5% buffered Formalin.

Larval abundances were calculated as number per 1,000 m^3 for each tow. The six sampling series were combined into three data sets, spring daytime samples (30 April and 14 May, NH10), summer daytime (2 and 13 July, NH5), and summer nighttime (2 and 6-7 July, NH5). In April and May the salinity profiles closely paralleled each other, with lower salinity at the surface, 30.5-31.0‰, than in deeper water, where salinities gradually increased to about 33-34‰ (Fig. 2a). Water temperatures above 50 m

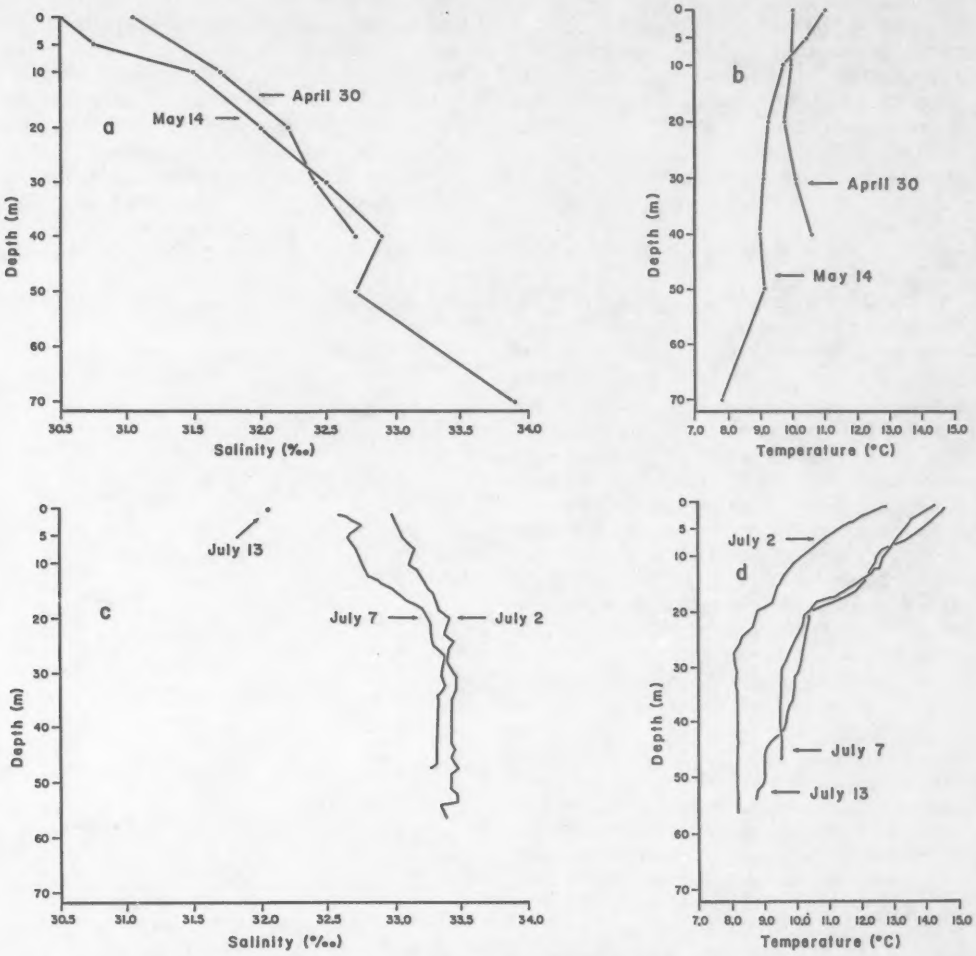

FIGURE 2.—Salinity and temperature profiles during the collections. a. Salinity profiles during the spring collections. b. Spring temperature profiles. c. Summer salinity profiles. d. Summer temperature profiles.

in April and May were about 9°-11°C (Fig. 2b). No thermocline was present. Thus, hydrographic regimes support grouping April and May samples together. Temperature and salinity profiles in April and May were typical for the winter Oregon hydrographic regime prior to the onset of late spring-early summer upwelling (Huyer 1977).

In July the salinity and temperature profiles differed from those in April and May (Figs. 2c, d). Salinities were more uniform in summer than spring throughout the water column, ranging from 32.0‰ at the surface to 33.4‰ below about 20 m (Fig. 2c). The temperature gradient in July was greater than in April and May due to warmer surface waters (Fig. 2d). Surface temperatures ranged from 12.8° to 14.6°C, decreasing with depth to about 8.2°-9.6°C at 40 m. A thermocline was present at about 10-20 m. Temperature and salinity profiles in July were typical of the summer Oregon hydrographic regime (Huyer 1977). Surface temperatures suggest that samples were not taken during active upwelling.

RESULTS

In this study, a total volume of 29,145.5 m^3 was filtered and 1,007 larvae, representing 33 taxa, were enumerated from 75 discrete depth tows. Larvae were most abundant in summer, with an abundance peak 10-30 m deep during daytime and 20-30 m deep during nighttime (Fig. 3). In spring, larvae were distributed relatively uniformly throughout the water column below 5 m with small abundance peaks at 10-20 and 40-50 m. During daytime in both spring and summer, larvae were least abundant at the surface (0-5 m), although abundance at the surface increased at night. The depth distribution at night also differed in having a secondary abundance peak near the bottom (50-60 m) and greater overall larval abundance than during the day.

The larval fish species were categorized as coastal (most abundance 2-28 km from the coast, see Tables 2, 3, and 4), or offshore (most abundant 37-111 km from the coast, see Tables 5, 6, and 7), according to larval assemblages described by Richardson and Pearcy (1977). Most larvae in this study were of the coastal assemblage because samples were collected at NH5 and NH10 (9.2 and 18.5 km from the coast, respectively). The spawning seasons of the dominant species off Oregon are discussed in Mundy (1984); most of the fall-winter spawning species were not represented in this study. Since many species were not abundant enough to demonstrate trends, only the dominant species will be discussed below.

Coastal Assemblage

Gadus macrocephalus, *Microgadus proximus*, *Isopsetta isolepis*, and *Psettichthys melanostictus* larvae were abundant in all three sampling periods (Tables 2, 3, 4, Fig. 4). *Gadus macrocephalus* larvae were most abundant during the day at 20-30 m in both spring and summer, but were very abundant in the deepest stratum (below 50 m) in night samples (Fig. 4). *Microgadus proximus* larvae do not show as clear a trend, but were most abundant in deeper water during summer, particularly at nighttime. In spring they were distributed throughout the water column. *Isopsetta isolepis* and *P. melanostictus* were also most abundant in nighttime samples. More *I. isolepis* larvae were found at 10-20 m in spring, whereas in summer they were collected throughout the water column, with abundance peaks near the bottom. *Psettichthys melanostictus* larvae were more abundant in summer than spring samples. During daytime in summer, *P. melanostictus* were most abundant below 10 m, whereas at nighttime, although found throughtout the water column, they were most abundant in waters shallower than 10 m (Fig. 4).

Seasonal abundance changes were observed for

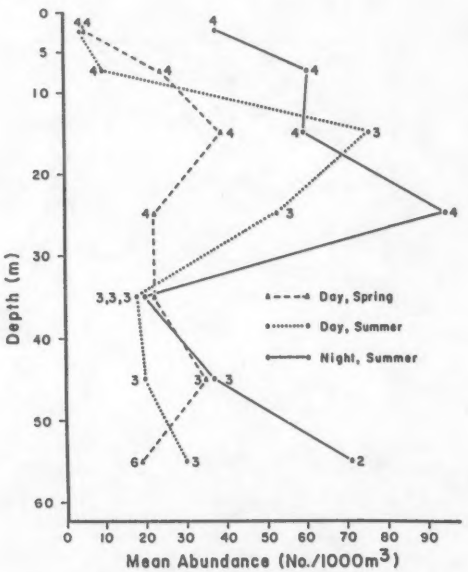

FIGURE 3.—Overall larval abundance (larvae per 1,000 m^3) for all collections. Numbers adjacent to data points indicate the number of samples taken.

TABLE 2.—Mean abundances (number per 1,000 m^3) for coastal larval species from spring (day only) samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Clupeidae								
Clupea harengus	—	—	1.76	2.36	1.25	0.75	—	0.87
Osmeridae								
Undetermined spp.	—	1.85	5.02	1.22	1.51	1.16	0.23	1.57
Gadidae								
Gadus macrocephalus	1.14	0.53	5.69	7.59	2.91	—	0.89	2.68
Microgadus proximus	1.13	2.04	3.87	2.97	0.73	2.95	0.45	2.02
Cottidae								
Artedius fenestralis	—	—	—	—	—	—	—	—
Artedius harringtoni	—	—	—	—	—	0.75	0.41	0.17
Artedius meanyi	—	—	—	—	—	—	0.44	0.06
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	2.60	0.37
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	0.23	0.03
Cyclopteridae spp. 1	—	—	—	0.74	2.29	3.64	0.45	1.02
Undetermined spp.	—	—	—	0.47	—	—	—	0.07
Bathymasteridae								
Ronquilus jordani	—	0.59	—	—	—	—	—	0.08
Ptilichthyidae								
Ptilichthys goodei	—	—	0.94	—	—	—	—	0.13
Bothidae								
Citharichthys stigmaeus	—	—	—	—	0.73	—	0.87	0.23
Pleuronectidae								
Isopsetta isolepis	0.49	1.79	7.78	2.86	—	1.29	0.66	2.12
Lepidopsetta bilineata	—	0.59	0.94	—	—	—	—	0.22
Parophrys vetulus	—	0.59	1.76	—	—	—	0.45	0.40
Psettichthys melanostictus	1.48	5.46	5.58	—	0.73	—	0.44	1.96

TABLE 3.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer day samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	—	—	—	—	—	3.69	0.53
Gadidae								
Gadus macrocephalus	—	—	1.38	12.01	1.08	1.09	—	2.22
Microgadus proximus	—	—	2.01	1.01	—	3.28	3.49	1.40
Cottidae								
Artedius fenestralis	—	—	1.00	1.15	—	—	—	0.31
Artedius harringtoni	—	0.68	4.54	3.30	2.18	2.19	3.39	2.33
Artedius meanyi	—	—	3.38	2.02	1.10	—	—	0.93
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	1.01	—	—	—	0.14
Cyclopteridae spp. 1	—	—	—	2.22	2.16	—	—	0.63
Undetermined spp.	—	—	2.16	4.18	1.08	2.18	6.05	2.24
Bathymasteridae								
Ronquilus jordani	0.63	0.70	2.01	1.01	—	—	—	0.62
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	1.00	—	—	—	—	0.14
Pleuronectidae								
Isopsetta isolepis	—	—	2.07	1.01	2.20	—	4.82	1.44
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	—	—	—	—	—	—	—	—
Psettichthys melanostictus	0.98	2.03	22.98	7.48	3.24	3.26	11.18	7.31

TABLE 4.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer night samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	4.42	15.15	4.56	—	0.75	1.12	3.71
Gadidae								
Gadus macrocephalus	—	—	—	0.82	3.16	8.11	22.98	5.01
Microgadus proximus	0.66	0.61	—	4.66	1.95	3.29	6.91	2.58
Cottidae								
Artedius fenestralis	3.20	—	0.78	1.57	—	0.75	2.60	1.27
Artedius harringtoni	1.35	4.41	5.44	11.30	0.73	1.27	1.40	3.70
Artedius meanyi	0.66	4.48	0.71	4.12	0.74	1.01	3.62	2.19
Clinocottus embryum	0.66	—	—	—	—	—	—	0.09
Cottus asper	—	—	—	—	—	—	—	—
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	2.50	0.36
Cyclopteridae spp. 1	—	—	0.77	0.79	—	—	—	0.22
Undetermined spp.	—	—	—	3.96	0.73	—	4.74	1.35
Bathymasteridae								
Ronquilus jordani	—	—	0.71	1.70	—	1.27	—	0.53
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	—	0.74	0.74	—	—	0.21
Pleuronectidae								
Isopsetta isolepis	—	2.57	1.63	6.50	2.64	10.90	1.12	3.62
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	0.66	—	0.71	—	—	—	—	0.20
Psettichthys melanostictus	24.63	31.37	13.65	18.86	7.78	6.07	6.91	15.61

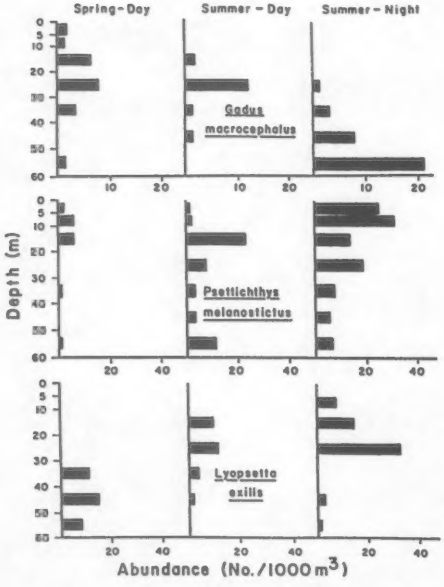

FIGURE 4.—Vertical abundance patterns of the three most abundant taxa (*Gadus macrocephalus*, *Psettichthys melanostictus*, and *Lyopsetta exilis*) during the three sampling periods.

Artedius and cyclopterid species. *Artedius fenestralis*, *A. harringtoni*, and *A. meanyi* were taken almost exclusively in the summer sampling period. All species were most abundant in nighttime samples. During the day, *A. harringtoni* larvae were distributed relatively uniformly throughout the water column from about 10 to 60 m, whereas at night most larvae were taken from the 5-30 m depth strata. Most cyclopterid larvae collected in spring were the larval type referred to as Cyclopteridae spp. 1 by Richardson and Pearcy (1977). Other cyclopterid species were more abundant in summer. Most cyclopterid larvae were collected below 20 m during both night and day, and in summer were abundant at the deepest sampling depths.

Osmerid larvae of undetermined species had a unique distribution pattern. They were abundant during spring, rare during summer daytime samples, and most abundant during summer nighttime samples. During both spring and summer, larvae were most abundant at the 10-20 m depth stratum.

Offshore Assemblage

Spring to summer differences in abundance patterns were more distinct for offshore larval species as compared with coastal species (Tables 5, 6, 7).

TABLE 5.—Mean abundances (number per 1,000 m^3) for offshore larval species from spring (day only) samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Offshore								
Engraulidae								
Engraulis mordax	—	—	—	—	—	—	—	—
Bathylagidae								
Bathylagus ochotensis	—	—	0.56	—	0.78	7.28	0.87	1.36
Bathylagus pacificus	—	—	—	—	—	—	0.22	0.03
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	0.75	—	0.11
Protomyctophum thompsoni	—	—	—	—	—	1.74	1.19	0.42
Stenobrachius leucopsarus	0.49	6.79	2.76	0.47	—	—	—	1.50
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	—	2.73	1.06	1.49	—	—	—	0.75
Bothidae								
Citharichthys sordidus	—	—	—	—	—	—	—	—
Pleuronectidae								
Glyptocephalus zachirus	—	—	1.06	—	—	—	—	0.15
Lyopsetta exilis	—	—	—	—	11.27	14.9	8.56	4.96
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	1.49	—	—	—	0.21

TABLE 6.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer day samples.

Species	Depth (m)							Mean
	0-5	5-10	10-20	20-30	30-40	40-50	>50	
Offshore								
Engraulidae								
Engraulis mordax	0.98	2.13	—	—	—	—	—	0.44
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	1.49	0.73	—	—	—	—	—	0.32
Scorpaenidae								
Sebastes spp.	—	0.65	3.03	1.08	1.10	—	—	0.84
Bothidae								
Citharichthys sordidus	—	0.73	—	—	—	—	—	0.10
Pleuronectidae								
Glyptocephalus zachirus	—	2.11	19.55	4.52	—	—	—	3.74
Lyopsetta exilis	—	—	10.03	11.53	4.38	2.13	—	4.01
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	—	—	1.10	—	0.16

Only *Sebastes* and *Lyopsetta exilis* larvae were abundant in all three sampling periods. *Sebastes* larvae were most abundant in nighttime samples, when they were mainly collected in shallow water (0-20 m). In both spring and summer daytime samples they were also in relatively shallow waters (5-40 m), although they were not abundant at the shallowest stratum (0-5 m). During day, *L. exilis* larvae were distributed in deeper water, particularly in spring, when all larvae were collected below 30 m (Fig. 3). At night, most *L. exilis* were shallower, between 5 and 30 m.

Two species, *Bathylagus ochotensis* and *Stenobrachius leucopsarus*, were collected only in spring samples. These two species were predominantly collected at different depths with *B. ochotensis* found

TABLE 7.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer night samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	4.09	3.76	—	—	—	—	—	1.12
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	3.86	0.68	2.38	0.82	—	—	1.12	1.27
Bothidae								
Citharichthys sordidus	—	—	0.78	—	0.74	1.27	10.27	1.87
Pleuronectidae								
Glyptocephalus zachirus	0.66	0.68	0.77	0.91	—	—	—	0.43
Lyopsetta exilis	—	8.28	15.05	32.99	—	3.53	1.12	8.71
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	0.71	—	—	—	1.12	0.26

in deeper water (40-50 m) and *S. leucopsarus* in shallow water (5-20 m).

Two species of larval flatfishes and *Engraulis mordax* were collected only in summer samples. *Glyptocephalus zachirus* were most abundant during day at 5-30 m, and *Citharichthys sordidus* at night below 50 m. *Engraulis mordax* larvae were collected only above 10 m. *Engraulis mordax* were most abundant at night when more than half were in very shallow waters, <5 m. During the day, more *E. mordax* were found at 5-10 m than at 0-5 m.

A relationship between larval size and depth was not evident for any species. Because of the low abundances of larvae, however, this relationship could not be adequately considered for most species. A change in larval size with season was demonstrated for the most abundant species (Table 8), with mean larval standard lengths of all species greater in summer than in spring samples. There were no obvious differences between the size of larvae caught in day and night summer samples.

DISCUSSION

Peak abundances of all taxa combined occurred at 10-30 m on all sample dates (Fig. 3) and characterized several individual taxa during the day, including *Clupea harengus*, Osmeridae, *Gadus macrocephalus*, *Sebastes* spp., and *Parophrys vetulus*, as well as *Lyopsetta exilis* and *Psettichthys melanostictus* in the summer. The 10-30 m depth range bracketed the lower boundary of the seasonal thermocline in July, although no thermocline was present in April-May (Fig. 2). This trend for the peak abundance of fish larvae to be centered near the thermocline is similar to that found in other regions (Ahlstrom 1959; Miller et al. 1963; Kendall and Naplin 1981).

The trend for most larvae to be found in midwater was similar to that described by Brewer et al. (1981) for their deepest stations off southern California. We did not find large concentrations of larvae near the bottom as they did, except at night, when gadids, cottids, cyclopterids, and pleuronectids were abundant. Our sampling gear was ineffective just above the bottom as compared with the roller-equipped gear used by Brewer et al. (1981).

Richardson and Pearcy (1977) found larvae to be most abundant at 0-10 m and least abundant at 51-100 m during late May off Oregon. We found larvae to be most abundant at 10-30 m. This difference may be due to differences in hydrography and station locations. Their station was 18 km offshore, closer to the shelf break where the depth of water was over 150 m deep. The faunal composition in each study was also different. Richardson and Pearcy (1977) captured more specimens of several surface-associated taxa than we did, including large *Clupea harengus*, *Stenobrachius leucopsarus*, *Ronquilus jordani*, and *Ammodytes hexapterus*. We captured higher densities of deeper dwelling taxa, including gadids and cottids. Several taxa taken in both studies had different distributions in each, including *Sebastes*

TABLE 8.—Ranges and mean standard lengths (mm) for dominant fish larvae. *N* = number of larvae; Min. = minimum; Max. = maximum.

Species	Spring: Day				Summer: Day				Summer: Night			
	N	Min.	Mean	Max.	*N*	Min.	Mean	Max.	*N*	Min.	Mean	Max.
Coastal												
Clupea harengus	10	7	8.2	9	0	—	—	—	0	—	—	—
Osmerid	17	3	7.1	17	3	29	33.1	38	35	23	31.8	40
Gadus macrocephalus	29	8	10.8	20	17	9	13.6	17	28	9	13.3	19
Microgadus proximus	22	6	10.9	19	9	11	21.3	36	18	6	18.4	33
Artedius fenestralis	0	—	—	—	2	11	12.0	13	8	10	11.6	13
Artedius harringtoni	2	6	6.5	7	15	5	8.2	13	33	5	8.6	14
Artedius meanyi	1	—	4.9	—	6	7	9.9	16	19	7	9.4	18
Radulinus asprellus	10	6	7.6	9	0	—	—	—	0	—	—	—
Liparid type 1	12	4	5.7	6	4	3	3.1	3	2	3	3.5	4
Liparid unknown	1	—	10.2	—	14	5	16.7	25	10	15	20.4	23
Ronquilus jordani	1	—	6.6	—	5	22	27.1	33	5	24	24.1	25
Isopsetta isolepis	22	4	8.9	21	9	10	20.0	23	28	7	16.1	23
Psettichthys melanostictus	—	3	7.0	22	41	9	20.0	27	150	8	20.8	28
Offshore												
Engraulis mordax	0	—	—	—	4	12	13.5	15	12	7	13.1	16
Bathylagus ochotensis	16	5	8.1	19	0	—	—	—	0	—	—	—
Stenobrachius leucopsarus	19	3	5.2	9	0	—	—	—	0	—	—	—
Sebastes spp.	8	4	4.7	6	6	4	14.6	18	12	12	16.0	18
Citharichthys sordidus	0	—	—	—	1	—	20.5	—	11	17	37.8	40
Glyptocephalus zachirus	2	13	25	37	22	14	29.9	39	4	22	34.5	50
Lyopsetta exilis	71	4	8.4	15	27	11	13.2	16	79	7	12.2	20

spp., Cyclopteridae spp. 1, and *Isopsetta isolepis*. These differences indicate the need for more extensive sampling before the variability of vertical distributions off Oregon can be understood, particularly as they relate to hydrographic conditions.

We found *Engraulis mordax* larvae entirely at 0-10 m. Brewer et al. (1981) found greater concentrations of *Engraulis* below 10 m, while Ahlstrom (1959) found *Engraulis* to be concentrated in the upper 23 m with some specimens occurring to 105 m. Off Oregon, *Engraulis* larvae are found concentrated at 0-20 m (Richardson 1973), in association with the Columbia River plume, a lens of warm, low salinity water usually 20-40 m deep (Richardson 1980). Our limited data suggest that *Engraulis mordax* larvae occur at depths that would place them within the plume, rather than beneath it or at its boundary. The vertical distribution suggests restriction to the warmest part of the water column (Fig. 2d); northern anchovies rarely spawn in waters with surface temperatures below 14°C (Lasker et al. 1981).

The seasonal differences in species composition between the April-May and July samples were those that would be expected in samples from winter and summer hydrographic regimes, except that *Artedius fenestralis* and *A. meanyi* have been taken in April and May of other years (Mundy 1984). The presence of *Clupea harengus*, *Radulinus asprellus*, myctophid, and bathylagid larvae only in April-May, during a winter hydrographic regime, is expected from previous studies (Richardson and Pearcy 1977; Mundy 1984).

Studies of day/night differences in the distribution of fish larvae are confounded by daytime avoidance of nets by larvae (Ahlstrom 1959). Daytime avoidance of nets is suggested in our study by the greater numbers of larvae taken during the night than day at all but two depth strata. The lack of length differences between larvae caught in day and night, however, and the fact that no taxa were taken only in night samples during July suggests that diurnal net avoidance was not related to taxon or size. The same comparisons with 70 cm bongo net samples (Richardson and Pearcy 1977) suggest that diurnal avoidance by large larvae was greater for bongo nets than for the Tucker trawl.

Evidence for vertical migration exists for several species in this study (Tables 3, 4, 6, 7). *Psettichthys melanostictus* abundance in surface waters (0-10 m) increased greatly at night (Fig. 4). *Engraulis mordax* were most abundant at 5-10 m than 0-5 m during the day, but more evenly distributed at night. This could be due either to vertical migration or net avoidance in the shallowest stratum during the day. Ahlstrom (1959), however, presented evidence for negative phototaxis by anchovy larvae, and Hunter and Sanchez (1976) demonstrated nighttime migration to the surface in larvae larger than 10 mm SL. Thus larvae migrate upwards at night, but are con-

strained to shallower water in the day as compared with the southern subpopulation.

The clearest case of vertical migration was that of *Gadus macrocephalus* (Tables 3, 4), which was most abundant at 20-30 m in the day and deeper than 50 m at night. The migration of this species was primarily responsible for the increased total abundance of larvae near the bottom at night (Fig. 3). This pattern of movement is similar to that observed for larval *Ammodytes personatus* by Yamashita et al. (1985), who suggested that this reverse vertical migration allowed feeding in daytime and avoidance of migrating predators at night. This nocturnal descent, not previously reported for *Gadus* larvae, should be confirmed with further sampling. *Gadus morhua* larvae 3.8-4.9 mm long move from deeper water in the day to 0-2 m at night, and descend in the water column with growth (Hardy 1978). Larvae of another gadid, *Melanogrammus aeglefinus*, are most common in the thermocline and their depth of greatest abundance fluctuates as the thermocline depth changes with rotary tidal currents, causing occasional descent in the water column at night (Miller et al. 1963).

Offshore taxa in Oregon coastal waters should occur in greatest numbers during onshore surface water transport during winter and early spring. This was true in our study for the mesopelagic Myctophidae and Bathylagidae, but not for other offshore assemblage taxa (Tables 5, 6, 7). Almost all of the bathylagid and myctophid larvae except *Stenobrachius leucopsarus* were found below 30 m. Ahlstrom's (1959) work confirms these general distributions; he found most larvae of the genera taken in this study (*Electrona* = *Protomyctophum*; *Lampanyctus* = *Stenobrachius*) at depths >56 m, beneath the thermocline, except *Stenobrachius*. He found *Stenobrachius* to have the shallowest distribution of all myctophid larvae in his study (0-41 m). Richardson and Pearcy (1977) also found *Stenobrachius* larvae to be in shallow waters (0-50 m) with many at 0-10 m during the day. The distribution of larval mesopelagic fishes, or other offshore taxa, cannot be related to the depth of onshore transport because virtually nothing is known about the depth of winter onshore transport off Oregon (Peterson et al. 1979; Huyer[4]). Both deep and surface dwelling larvae of mesopelagic fishes collected in our study appear to be transported onshore, however, suggesting that transport occurs over a broad depth range off Oregon.

[4]A. Huyer, Associate Professor, Oregon State University, Corvallis, OR 97331, pers. commun. 29 September 1983.

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

BREWER, G. D., R. J. LAVENBERG, AND G. E. MCGOWAN.
1981. Abundance and vertical distribution of fish eggs and larvae in the southern California bight: June and October 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:165-167.

CLARKE, M. R.
1969. A new midwater trawl for sampling discrete depth horizons. J. Mar. Biol. Assoc. U.K. 49:945-960.

HARDY, J. D., JR.
1978. Family Gadidae: *Gadus morhua* Linnaeus, Atlantic cod. *In* Development of fishes of the Mid-Atlantic Bight, an atlas of egg, larval + juvenile stages. Vol. II, p. 236-259. U.S. Dep. Inter., Fish Wildl. Serv.

HUNTER, J. R., AND C. SANCHEZ.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

HUYER, A.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442-453.

KENDALL, A. W., JR., AND N. A. NAPLIN.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull., U.S. 79:705-726.

LAROCHE, J. L., AND S. L. RICHARDSON.
1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455-476.

LASKER, R., J. PELÁEZ, AND R. M. LAURS.
1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy *Engraulis mordax*. Remote Sens. Environ. 11:439-453.

MILLER, D., J. B. COLTON, JR., AND R. R. MARAK.
1963. A study of the vertical distribution of larval haddock. J. Cons. Perm. Int. Explor. Mer 28:37-49.

MUNDY, B. C.
1984. Yearly variation in the abundance and distribution of fish larvae in the coastal upwelling zone off Yaquina Head, Oregon from June 1969 to August 1972. MS Thesis, Oregon State Univ., Corvallis, 158 p.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1:175-203.

PETERSON, W. T., C. B. MILLER, AND A. HUTCHINSON.
1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26A:467-494.

RICHARDSON, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71: 697-711.
1980. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.
RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.
ROTHLISBERG, P. C., J. A. CHURCH, AND A. M. G. FORBES.
1983. Modelling the advection of vertically migrating shrimp larvae. J. Mar. Res. 41:511-538.
SCHLOTTERBECK, R. E., AND D. W. CONNALLY.
1982. Vertical stratification of three nearshore southern California larval fishes *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*. Fish. Bull., U.S. 80:895-902.
SHANKS, A. L.
1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311-315.
WROBLEWSKI, J. S.
1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. Deep-Sea Res. 29A:665-686.
YAMASHITA, Y., D. KITAGAWA, AND T. AOYAMA.
1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel, *Ammodytes personatus*. Bull. Jpn. Soc. Sci. Fish. 51:1-5.

DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC

DAVID W. K. AU AND WAYNE L. PERRYMAN[1]

ABSTRACT

Research-ship surveys by the Southwest Fisheries Center provided information on the distributions of spotted, spinner, striped, and common dolphins in the eastern tropical Pacific. The main surveys were conducted from January to March during 1976, 1977, 1979, and 1980. Two ships were used per survey, and together they overlapped most areas in the eastern Pacific where dolphins and yellowfin tuna are jointly fished by purse seiners.

The spatial distribution of sightings and of sighting rate of these species show a complementarity to their patterns, although there is a broad overlap. Spotted and spinner dolphins occurred primarily in tropical waters north of the Equator, but also in the seasonal tropical waters south of the Galapagos Islands. These dolphins were relatively infrequent along the Equator, off Costa Rica, and northern South America. Common and striped dolphins tended to be more frequent in these same areas of less frequent spotted and spinner dolphins.

The differences in habitats of these two species pairs can be described in oceanographic terms. Spotted and spinner dolphins are primarily in Tropical Surface Water, centered off southern Mexico and extending westward along lat. 10°N, where thermocline "ridging" and relatively small annual variations in surface temperature are features. Common and striped dolphins appear to perfer equatorial and subtropical waters with relatively large seasonal changes in surface temperature and thermocline depth and with seasonal upwelling.

The species composition of various areas in the eastern tropical Pacific supports the contention of two major communities. South of where spotted and spinner dolphin schools predominate (along with Risso's, bottlenose, and rough-toothed dolphins), striped and common dolphins and also pilot whales become increasingly important. Observations along the Equator also suggest a fauna different from that of the Tropical Surface Water that is most characterized by spotted and spinner dolphins.

A trophic basis to these faunal differences is suggested by the interactions with fish and birds. Assuming the birds indicate co-occurring tuna, only the spotted and spinner dolphins are commonly found with fish. The distribution of these dolphins as they co-occur with bird flocks and tuna indicates that this interspecific association is confined primarily to the Tropical Surface Water and is a characteristic feature of its epipelagic community.

The eastern tropical Pacific Ocean supports productive tuna fisheries as well as an abundant and diverse cetacean fauna. Tuna fishermen there take advantage of the fact that tuna and dolphins frequently swim together. In the "porpoise-tuna" fishery for yellowfin tuna, *Thunnus albacares*, spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, are temporarily caught by purse seiners in order to take the associated tuna. Striped and common dolphins, *S. coeruleoalba* and *Delphinus delphis*, are caught to a lesser extent for the same reason. These dolphins suffer incidental mortality in the fishery and, because of the resulting concern, the Southwest Fisheries Center has been studying their populations to better advise on their management (Smith 1983). Learning about their habitats is one aspect of these studies.

Perrin (1975a), using the information collected mainly aboard tuna seiners, first showed that the geographic distributions of spotted, spinner, and striped dolphins in the eastern Pacific are extensive, stretching westward from the American coasts past long. 145°W at about lat. 10°N and also dipping south and southwest of the Galapagos Islands. Evans (1975) showed that the common dolphin occurs offshore of Central America to about long. 112°W and also along the Equator, westward past the Galapagos Islands. Recent summaries of available information (Au et al. 1979[2]; Scott 1981; Perrin et al. 1983) have shown that the distributions of these dolphins are even more extensive than originally perceived. Indeed the species have been reported from localities across the entire Pacific (Alverson 1981).

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[2]Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Admin. Rep. LJ-79-43, 59 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

The purpose of this paper is to describe the January-March distributions of schools of spotted, spinner, striped, and common dolphins as determined from research ship surveys. Being independent and distinct from data collected by observers aboard tuna seiners, these survey data enable a separate evaluation of habitats and ecological relationships. The distributions derived will be discussed in terms of habitat features and interspecific associations including those of other cetaceans, yellowfin tuna, and certain seabirds. We propose that two major cetacean communities can be recognized, centered broadly about the tropical and about the equatorial-subtropical surface water provinces (Fig. 1).

METHODS

The Southwest Fisheries Center conducted or participated in 17 research cruises studying cetaceans between 1976 and 1981. Eight major cruises were carried out between January and March of 1976, 1977, 1979, and 1980, with the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. During these surveys, schools of all cetacean species encountered (at least 23 species in the areas of interest) were approached to allow close observation. The combined cruise tracks of these January-March surveys formed an extensive coverage of the eastern tropical Pacific and included areas not frequently searched by fishing vessels (Fig. 2). The latter are the equatorial waters and areas both south of lat. 8°N and west of long. 110°W. The cruise tracks during any particular year were chosen to investigate certain aspects of dolphin distribution, e.g., the intensive surveys during 1979 off southern Mexico and central America constituted a joint aircraft-ship survey of the nearshore habitat. The remaining other nine cruises were either for special studies or of ships of opportunity. In the latter case, the ships did not usually divert course to inspect cetacean schools that were sighted.

Cetacean observations from a research ship were conducted by scanning the waters ahead and to the sides of the ship through 20 × 120 mm USN MK-3

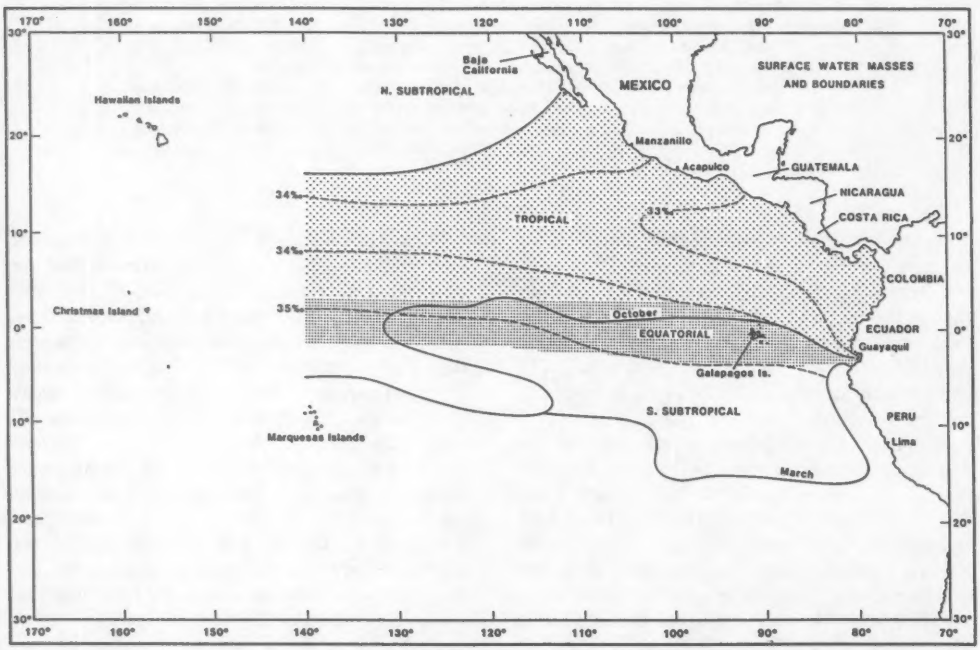

FIGURE 1.—Surface water masses and boundaries of the tropical ocean in the eastern Pacific, based on Wyrtki's (1964a, 1967) analysis to long. 140°W. Boundaries are a function of the 24°C surface isotherm and the 1°C/10 m thermocline gradient. Notice that in October the southern boundary to the eastern tropical ocean lies mostly north of the Equator, while in March this boundary lies far to the south so that southern subtropical waters become tropical.

or 25 × 150 mm Fuji binoculars, mounted both port and starboard either on or above the flying bridge. The sighting distance to the horizon was about 7.0 and 5.5 nmi for the *David Starr Jordan* and *Townsend Cromwell* respectively. Both ships cruised at about 10 kn (18.5 km/h). The cetacean search-day generally started at 0600 and ended 1800, with two teams, or watches, alternating. In 1976 and 1977 the watches were each 2 or 3 h long, depending on the ship. In 1979 and 1980 they were all standardized to 3 h. There were two experienced persons on each watch, who alternated each hour between the port and starboard binoculars. A third person sometimes helped in record keeping, obtaining supplementary data, and temporarily relieving the other watch members. The peripheral data collected included bathythermograms, surface temperature and salinity, weather observations, sighting condition measurements, sighting effort, and observations on fish and birds.

When a cetacean school was sighted, its angle relative to the ship's heading was measured and its distance from the ship estimated. The ship then approached the school for closer observation. School size was estimated and the species identified.

The reader is cautioned that the distributions to be described are based upon relatively few sightings of schools (Table 1) and that they pertain to the January-March season specifically. Though the pattern of sampling was widespread, the actual area surveyed was a very small fraction of the huge area

TABLE 1.—Summary of school sizes for spotted, spinner, striped, and common dolphins from the January-March research cruises of 1976, 1977, 1979, and 1980.

		Arithmetic		Geometric	
Species	n	$\bar{x}$	s	$\bar{x}$	s^1
Spotted[2]	157	148.52	300.93	65.55	3.56
Spotted and spinner	79	357.42	444.50	211.67	2.93
Spinner[3]	44	228.39	291.54	107.05	3.88
Striped	187	60.84	69.78	40.74	2.56
Common	98	261.16	484.64	108.47	3.72
Total[4]	565				

[1]Standard deviation factor for the geometric mean.
[2]Total spotted dolphin schools is 157 + 79 = 236.
[3]Total spinner dolphin schools is 44 + 79 = 123.
[4]Additionally, there were 838 school sightings of unidentified and other species of dolphins (Delphinidae) and 543 school sightings of whales (Balaenopteridae, Ziphiidae, and Physeteridae).

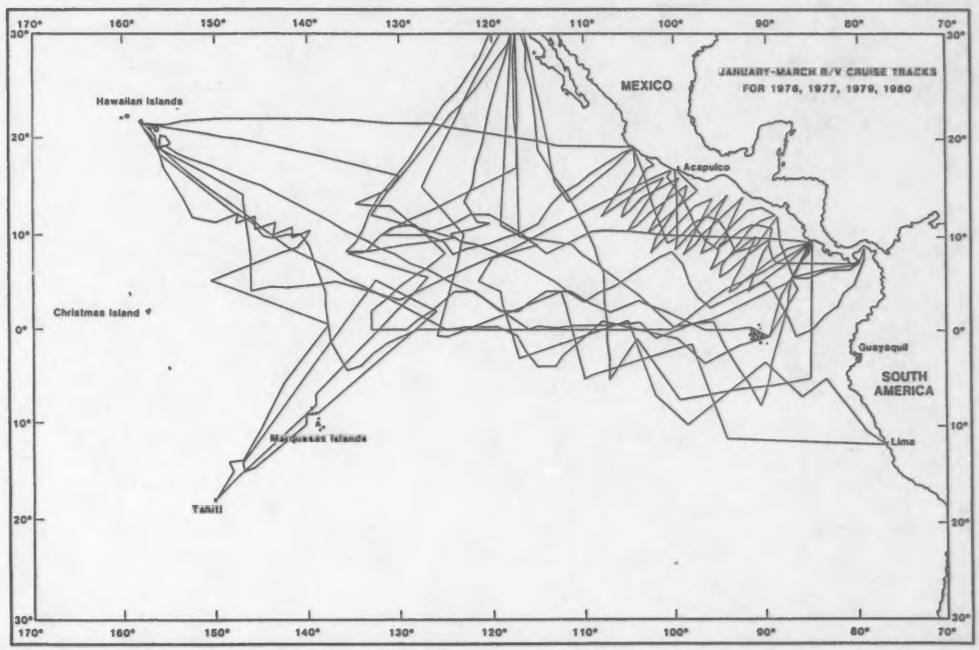

FIGURE 2.—Cruise tracks of the January-March cruises by RV *David Starr Jordan* and RV *Townsend Cromwell*. These cruises took place in 1976, 1977, 1979, and 1980.

of the eastern Pacific. The patterns of species distribution we describe will not always be obvious. Nevertheless there is evidence from other distribution studies, using data collected from the fishery, that these patterns are real (Perrin et al. 1983).

The results described in this paper are based upon our personal experiences at sea where the procedure of investigating all cetacean schools and continuously monitoring the physical and biotic environment enabled the development of an ecological understanding of these dolphins. Continuity in these studies was provided by the fact that on each ship there was at least one experienced observer who participated during all cruise years. We present our results as an independent, research-ship based, assessment of species distributions and habitat areas.

RESULTS

Distribution and Relative Abundance of Dolphin Schools

Plots of the sighting localities of schools of spotted, spinner, striped, and common dolphins, obtained during the January-March research cruises, show the geographical distributions of these species during the northern winter season. Table 1 summarizes the numbers and sizes of the schools which were identified and studied. Geographic locations referred to in the text can be found in Figure 1.

Spotted and spinner dolphins are often in mixed schools (33.5% of spotted dolphins schools also contained spinner dolphins, Table 1), and so the sightings of spotted or of mixed spotted plus spinner dolphin schools are shown together (Fig. 3). Most of the mixed schools were encountered off southern Mexico, where the eastern form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) usually accompanied spotted dolphins (cf. Figs. 3, 4). Mixed schools were uncommon along the Equator, as was the spotted dolphin itself, especially west of long. 110°W. Large schools (>300 individuals) of spotted dolphin were widely scattered, but tended to be more common off southern Mexico. Westward extensions of distribution appeared to occur as three main lobes: about lat. 10°n, between lat. 0° and 5°N, and between lat. 2°S and 5°S.

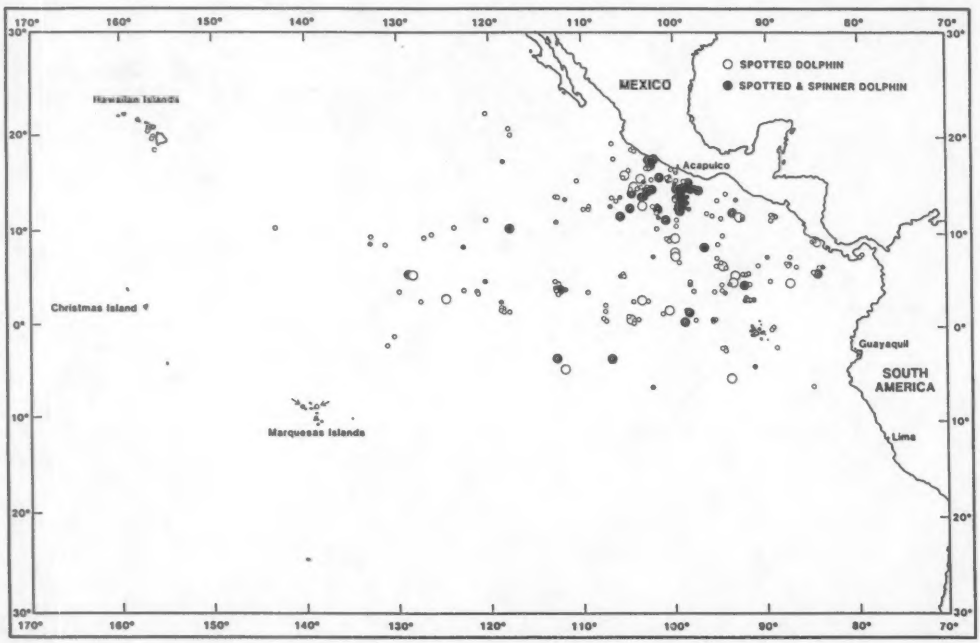

FIGURE 3.—Distribution of spotted and spotted plus spinner dolphin schools seen during the January-March research cruises. Larger circles indicate schools of >300 animals.

The spinner dolphin appears to be distributed like the spotted dolphin, with westerly extending lobes of distribution in similar latitudes (Fig. 4). Schools were infrequent along the Equator, more so than were those of spotted dolphin. The eastern spinner was encountered frequently off southern Mexico, where its main population center appeared to be relatively localized. However, eastern spinner dolphins were seen as far offshore as long. 126°W near lat. 10°N and also nearly to the Equator within a broad, 600 nmi coastal belt off Central America. The whitebelly form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) occurred in a broad range north and south of the Equator and at the southern and western portions of the total spinner dolphin range. Large schools (>300) were seen mostly off southern Mexico (eastern spinner) and south of the Equator (whitebelly spinner).

Striped and common dolphins seem to have a distribution pattern qualitatively different from that of spotted and spinner dolphins (Fig. 5). A distinct distributional lobe, consisting primarily of common dolphins, occurred off Baja California, with extensions around the Revilla Gigedo Islands (ca. lat. 19°N, long. 111°W). Between lat. 5° and 12°N, off Central America, there was a second lobe made up of both species. This lobe attenuated to the west along lat. 10°N, but appeared to re-intensify past long. 130°W. Only striped dolphins were seen in the intermediate interval between long. 100°W and 130°W along this lobe. A third lobe appeared to originate off Peru. It merged somewhat with the outer portions of the Central American lobe, and then extended westward along the Equator. Equatorial waters were frequented by both species out to about long. 100°W, beyond which striped dolphins apparently predominate. The striped dolphin is the more widespread of the two species; however, its school sizes are small (Table 1). Large schools (>300) of the common dolphin occurred within each of the three main centers of its distribution.

The above sighting data were adjusted to show the distributions of relative abundance of schools by correcting for searching effort. Effort is calculated as miles searched = time searched × ship speed. Relative abundance of schools was expressed as schools per 100 nmi searched (approximately the

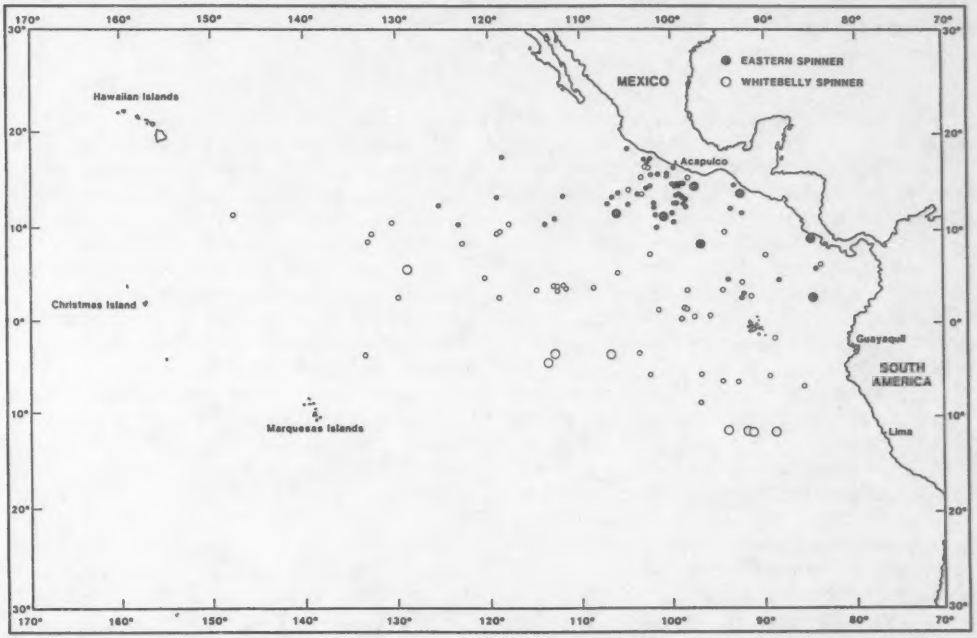

FIGURE 4.—Distribution of spinner dolphin schools, eastern and whitebelly forms, seen during the January-March research cruises. Larger circles indicate schools >300 animals.

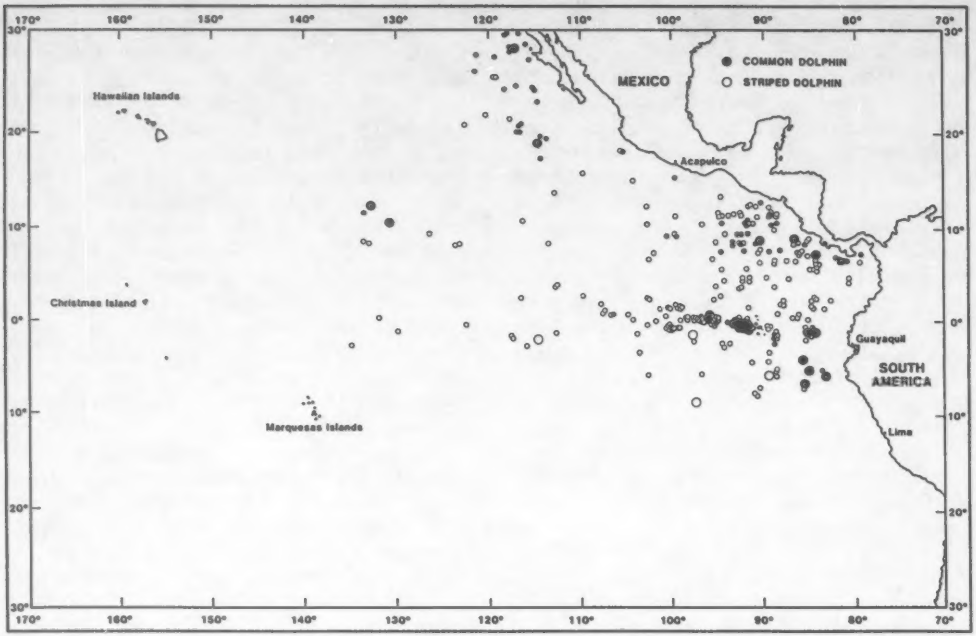

FIGURE 5.—Distribution of striped and common dolphin schools seen during the January-March research cruises. Larger circles indicate schools >300 animals.

distance searched during 1 d). Data for days during which the Beaufort wind force was equal to 4 (11-16 kn) for more than 50% of the time, or averaged more than 4, were not used. Only schools sighted at distances not more than 3 perpendicular nmi from the ship's track and not more than 5 radial nmi distant were considered, to reduce the effects due to distance on sightability. The latter criterion was not applied to the 1976 cruises, because the radial distances then were frequently overestimated. An areal smoothing procedure that consisted of calculating the average number of schools per 100 mi searched within sequential, overlapping 5° squares was employed. Sequential squares were offset 2.5° in latitude and longitude, so that each was wholly overlapped by 25% of the area of each of four adjacent squares. A day's sighting rate was assigned to a particular square if more than 50% of the search effort occurred therein, and the value was plotted at the center point of that square. If the search effort fell equally in two squares, the day's results were assigned to both squares. These moving, areal means of sightings per 100 nmi searched were plotted and contoured. Contouring (and interpolation) constituted a second level of areal smoothing.

The maps so generated describe the distribution of relative abundance of species schools as surveyed during January to March. These relative abundance data were combined for spotted and spinner dolphins and for striped and common dolphins, both because these species pairs had similar distributions and because pooling gave desirable sample sizes.

The combined spotted and spinner dolphin map (Fig. 6) shows some patterns already noted from the school distribution. These schools appeared relatively more abundant off southern Mexico (mostly spotted and eastern spinner dolphins) and again along an east-west band just north of the Equator, especially west of long. 105°W. Another band of greater abundance occurred south of the Equator. Spotted and spinner dolphins appeared less abundant just west of Costa Rica, off the coast of northern South America, and along the Equator. A weak lobe of higher relative abundance extended west of long. 120°W broadly about lat. 10°N.

Striped and common dolphins show a relative abundance pattern in which areas of higher density tend to be complementary to that of spotted and

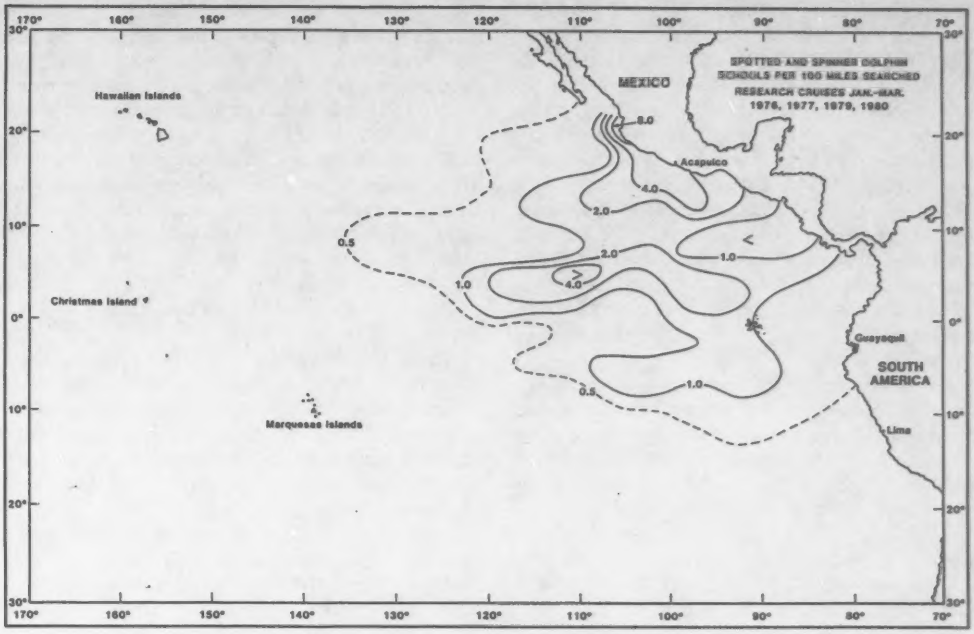

FIGURE 6.—Distribution of relative abundance of spotted and spinner dolphins, inferred from data of the January-March research cruises. Hawaiian and Marquesan sightings are not considered.

spinner dolphins (Fig. 7). Conspicuous lobes extended from off Baja California and also broadly from the coasts of Central America and northern South America out to and along the Equator. Within the latter lobe, centers of higher relative abundance occurred west of Nicaragua and Costa Rica and west of the Galapagos Islands, all areas where reduced abundance of spotted and spinner dolphins occurred. The Galapagos area and the lobe off Baja California were dominated by the common dolphin (cf. Fig. 5).

Dolphins of Tropical Water and Upwelling-Modified Water Habitats

The areas of greater frequency of spotted and spinner dolphins during January-March are the typical tropical waters of the eastern tropical Pacific. These waters are underlain by a sharp thermocline, generally >2°C/10 m, at depths usually much <50 m. The surface temperatures are >25°C, and the salinities <34‰. Such tropical waters are defined by Wyrtki (1966, 1967) as Tropical Surface Water (see Fig. 1). In particular the warm "Inner Tropical" Waters (Wyrtki 1964a) lying primarily north of the Equator comprise the major habitat of spotted and spinner dolphins (Fig. 6). The waters south of the Equator, where the relative abundance of these dolphins is also higher, are seasonally tropical, and are therefore called southern Subtropical Surface Water (Wyrtki 1966, 1967). These waters, occurring approximately south of lat. 2.5°S, have surface salinities >35‰, and during January-March (southern summer), warm to more than 26°C over a shallow, sharp thermocline. Since spotted and spinner dolphins occur there frequently, at least during January-March, it appears that spotted and spinner dolphins prefer all waters whose characteristics are, or become, tropical in the eastern Pacific. However the primary habitat appears to be the "Inner" Tropical Waters north of the Equator.

In contrast striped and common dolphins appear to prefer waters with more variable conditions during January-March. Their most important habitat appears to be broadly centered about equatorial waters (Fig. 7). This band of distribution extends into the central Pacific along the Equator. In the east it broadens widely to include Tropical Water off Cen-

tral America and Subtropical Water off Peru. The equatorial distribution is in Equatorial Surface Water (Wyrtki 1966, 1967), a transitional water mass straddling the Equator and characterized by salinities between 34 and 35‰, upwelling, and a relatively weak thermocline. These waters are markedly cooled from June to December (southern winter-spring) by increased upwelling and by advection from the Peru Current. In the Subtropical Water habitats of striped and common dolphins, both off Peru and Baja California, there are also large seasonal changes in temperature structure and effects from upwelling. Finally the Tropical Water habitat in the Central American Bight is notably variable (below).

The waters we call the "Central American Bight" (roughly, the near coastal waters from Guatemala to Ecuador) constitute the most important area of overlap for spotted, spinner, striped, and common dolphins, but this overlap is not balanced among the species. These waters are tropical, but they are the most variable within the Tropical Surface Water province. The Equatorial Countercurrent, flowing eastward between lat. 4°N and 10°N, terminates and turns there, creating a complex circulation. The annual north-south migration in these latitudes of the Intertropical Convergence Zone, where north and south trade winds meet, bring southerly winds, rain, reduced salinity, and an intensified Countercurrent during the second half of the year (Bennett 1966; Wyrtki 1967, 1974; Forsebergh 1969). Later during the northern winter (January-March), northeasterly winds blow across Central America from the Atlantic, producing coastal upwelling, wind stirring, and more complex temperature patterns. The Costa Rica Dome, a localized, offshore upwelling at about lat. 8°N, long. 90°W (Wyrtki 1964b), also may be seasonally intensified (Hofmann et al. 1981).

These variable Central American Bight waters appear to have more abundant schools of striped and common dolphins than of spotted and spinner dolphins (cf. Figs. 3-7). It seems that all areas with greater concentration of striped and common dolphins have highly variable oceanographic features that are "upwelling-modified".

In spite of the rather strong overlap in distribution among the four dolphin species in the Central America Bight, the biogeographic distinction, including the relationships to environment, between

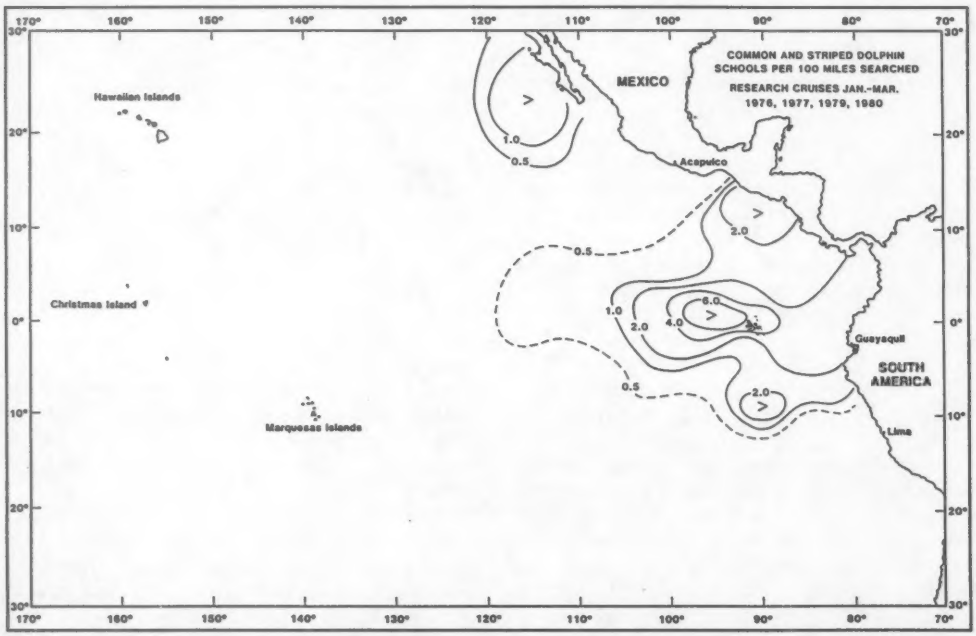

FIGURE 7.—Distribution of relative abundance of striped and common dolphins, inferred from data of the January-March research cruises.

the spotted and spinner dolphins of the Tropical Water and the striped and common dolphins of the Upwelling-Modified Water may be quite apparent. This was the case during the intensive winter surveys of 1979 in the Central American Bight, shown in Figure 8. Superimposed in the figure are contours of the 20°C isotherm depth (essentially the thermocline depth) which were obtained from expendable bathythermograph probes dropped at 30-60 mi intervals (55.6-111.1 km). Notice that spotted and spinner dolphins were encountered mainly off southern Mexico, where the deeper 20°C isotherms indicated the occurrence of a large surface lens of warm water. The warmest surface waters in the eastern tropical Pacific normally occur in this area; the thermocline gradient is weaker, and the annual variation in surface temperature is relatively small (Wyrtki 1964a). In the more variable tropical waters of the Central American Bight, where the thermocline had shoaled or ridged to <60 m, both these species were seen too. However, striped and common dolphin schools predominated, especially near the shallower isotherms that mark the location of the Costa Rica Dome. Finally the equatorial distribution of primarily striped and common dolphins was evident. The sampling suggested that Subtropical Waters south of the Galapagos Islands were probably also important to these latter two species. A 1977 aerial survey of cetaceans in these waters off Central America (SWFC 1977[3]) obtained results similar to those just described.

Though there appear to be large-scale geographic differences in the habitats of spotted and spinner dolphins and of striped and common dolphins, there was no evidence of negative association among these species. The frequency of days in the Central American Bight, both in 1979 and 1980, with different combinations of these species encountered, are summarized in Table 2. There was no evidence, using chi-square contingency tests for association among spotted and/or spinner dolphins and striped or common dolphins, that the species were not occurring independently on any particular day.

Our contention that spotted and spinner dolphins and striped and common dolphins differentially inhabit waters of different oceanographic characteris-

[3]Southwest Fisheries Center (SWFC). 1977. Aerial survey trip report January - June 1977. Admin. Rep. No. LJ-78-01, 73 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

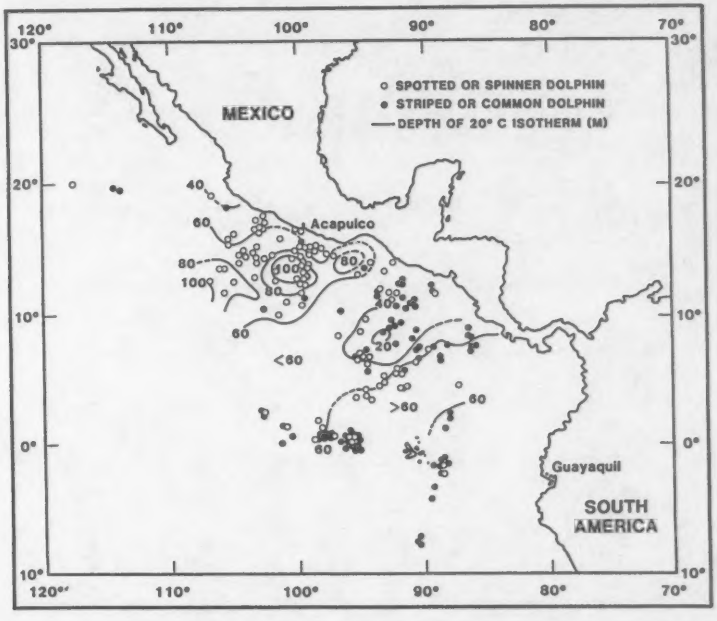

FIGURE 8.—Distribution of dolphin schools by species type in the Central American Bight, with reference to the depth of the 20°C isotherm. Data are from the January-March cruises of 1979.

TABLE 2.—Number of days according to combinations of four species of dolphins that were encountered in the Central American Bight.

		Spotted and/or spinner				Striped		Common	
Year	Area[1]	Alone	With striped	With common	With striped + common	Alone	With common	Alone	None of these spp.
1979	N	17	2	0	0	1	1	1	6
	S	6	7	0	4	6	1	6	8
1980	N	9	2	0	0	0	0	0	0
	S	5	5	1	4	6	3	3	7

[1]Northern (N) and southern (S) areas are partitioned to illustrate species differences by area; the dividing line is perpendicular to the coast at lat. 16°N.

tics is supported by physical environmental measurements. The data indicated a species differential with respect to waters with temperature ≥25°C and salinities ≤34.5‰, and waters of <25°C and >34.5‰. The former is primarily Tropical Surface Water and the latter primarily Equatorial-Subtropical Surface Water. Of 217 spotted and/or spinner dolphin schools encountered during the January-March cruises, and having associated temperature and salinity measurements, 80.6% were in this Tropical Surface Water, while only 19.4% were in the Equatorial-Subtropical Surface Water. In comparison 53.7% of 229 similarly observed schools of striped and/or common dolphins were in the Tropical Surface Water and 46.3% were in the Equatorial-Subtropical Water. The differential in percentages by species pair reflects the more uniform "Inner Tropical" Surface Water habitat of spotted and spinner dolphins and the importance to striped and common dolphins of both the variable Tropical Water off Central America and the variable waters along the Equator, west of Peru, and southwest of Baja California.

Because the school sighting data are represented by many combinations of temperature and salinity from various areas, it is useful to summarize these results in terms of an integrated measure of temperature and salinity, i.e., sigma-*t*, a measure of water density (see Sverdrup et al. 1942). Table 3 lists the numbers and percentages of spotted and spinner and of striped and common dolphins according to their occurrence at different intervals of sigma-*t*. The percentages of striped and common dolphin schools were higher than that of spotted and spinner dolphin schools for sigma-*t* ≥22.5 (primarily Equatorial-Subtropical Water). The opposite was true for sigma-*t* <22.5 (primarily Tropical Water). The difference in percentage distribution by species pair is significant ($P < 0.01$, Kolmogorov-Smirnov test).

Seasonal Features of Habitats

It is not clear how dolphin populations are affected by seasonal changes in the environment, although the available data suggest what may happen. The far offshore habitat of spotted and spinner dolphins, between long. 120°W and 140°W at about lat. 10°N, is an important "porpoise-tuna" fishing area during

TABLE 3.—Percent distribution of dolphin schools[1] according to surface water density (sigma-*t*).

sigma-*t*	Spotted	Spinner[2]	Total	%	Striped	Common	Total	%
+18.5-19.0					2		2	0.9
+19.0-19.5	2	1	3	1.4	5		5	2.2
+19.5-20.0	6		6	2.8	8		8	3.5
+20.0-20.5				0.0	2	1	3	1.3
+20.5-21.0	5	2	7	3.2	6	2	8	3.5
+21.0-21.5	16	12	28	12.9	11	2	13	5.7
+21.5-22.0	43	28	71	32.7	27	6	33	14.4
+22.0-22.5	12	32	54	24.9	26	19	45	19.7
+22.5-23.0	15	6	21	9.7	22	8	30	13.1
+23.0-23.5	8	11	19	8.8	39	15	54	23.6
+23.5-24.0	2	4	6	2.8	10	3	13	5.7
+24.0-24.5	2		2	0.9	6	6	12	5.2
+24.5-25.0					1	2	3	1.3
+25.0-25.5								
Total	111	96	217	100	165	64	229	100

[1]January-March, research cruises, 1976, 1977, 1979, 1980.
[2]Includes mixed spinner + spotted dolphin schools.

the spring and summer months (Calkins 1975). However there is little information from that area during the winter months (when there is little fishing), except for results from the January-March research cruises, which indicated that population densities there were not high (Fig. 6). This suggests a summer buildup in the concentration of these dolphins. This is likely because the offshore habitat is centered close to or along the divergence zone at the northern boundary of the North Equatorial Countercurrent, where the thermocline ridges and biological production is increased (Cromwell 1958). During the northern summer, the trade winds over the offshore habitat abate, ridging intensifies (Wyrtki 1964a, 1974), and porpoise-tuna fishing expands west of Clipperton Island (at ca. lat. 10°N, long. 109°W). The increase in fishing may be due to better weather, but possibly also to an increased abundance of dolphins and tuna.

The seasonal change in environment of the eastern tropical Pacific most likely to affect the distribution of dolphins is that due to the movement of the southern border of the tropical waters. During the northern winter, tropical conditions usually extend to about 15° south of the Galapagos Islands, when a shallow surface layer of warm water develops over what is actually Subtropical Water. During the northern summer, the cool Peru and South Equatorial Current strengthen, and a conspicuous thermal front, marking the southern boundary of Tropical Surface Water, usually develops. This Equatorial Front (Wyrtki 1966) is located a few degrees north of the Equator except for a short section east of the Galapagos Islands.

We studied the relationship of the Equatorial Front to dolphin populations during an October-November 1977 cruise of the *David Starr Jordan*. The Equatorial Front was conspicuous, as were the effects of the cool Peru and South Equatorial Currents (Fig. 9). Only 4 of 27 sightings of spotted and spinner dolphins schools in the equatorial region occurred in the cool, Equatorial and Subtropical Waters south of the front. The majority of the remaining 23 sightings were along the Equatorial Front, at the southern border to the warm Tropical Surface Water. These same species had occurred throughout these southern waters during January to March (Figs. 3, 4), when sea surface temperatures of 25°C or more prevailed over this entire area. The apparent redistribution of dolphin schools along the warm edge of the Peru Current and Equatorial Front appeared to be restricted to the spotted and spinner species, suggesting their seasonal movements away from cool southern waters. By implication these same dolphin species may migrate into southern waters during the warm season. Seasonal movements of dolphins (unidentified) in the southern waters is also suggested by results from the 1967 and 1968 EASTROPAC cruises (Love 1971, 1972). On the other hand, we did see during the October-November cruise four schools of spotted and spinner dolphins in cool Subtropical Water, and observers aboard tuna seiners have also reported these same species there during the cool season.

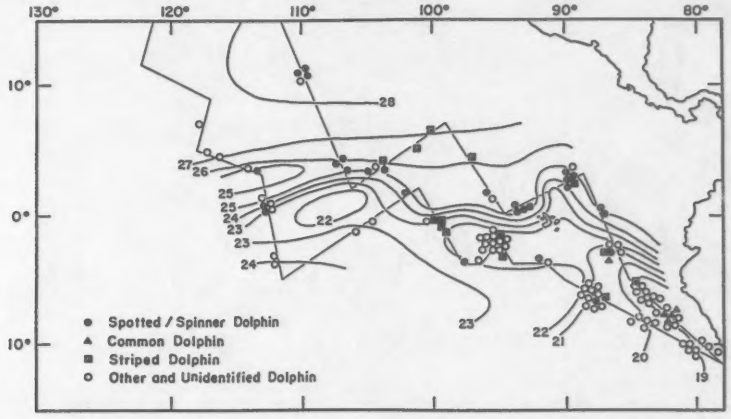

FIGURE 9.—Distribution of dolphin schools in the equatorial region during October-November 1977, relative to surface isotherms (°C). Notice the Equatorial Front or zone of rapid temperature change just north of the Equator. Clumping of sightings along the track is due to nighttime travel by ship. "Other" dolphins are primarily pilot whales.

Dolphin Communities

The habitat differences discussed also apply to other delphinid species, so that there seem to be different communities of dolphins in the eastern Pacific. To show how the cetacean communities differ between the habitats dominated by spotted and spinner and by striped and common dolphins, the eastern Pacific was divided into Areas I and II (Fig. 10, inset) that separate the main habitat areas of these two species pairs. Area I is primarily Tropical Surface Water and includes most areas where thermocline ridging is a dominant physical feature. Area II is primarily Equatorial-southern Subtropical Surface Water, but also includes the wedge-shaped area of variable Tropical Water in the Central American Bight. Area II comprises most of the waters we have called Upwelling-Modified.

In each of these two areas, only schools sighted at ≤1.0 nmi perpendicular to the ship's tracks were listed. This requirement was imposed so that percent species composition could be based on species schools, that to the largest practical degree, could all be sighted with equal probability, if present. The change in "sightability" with distance is different for each species because of differences in behavior, coloration, size, etc.

Our data indicate that the species composition of delphinids is different in these two areas. Percentage composition was determined for spotted; spinner; striped; common; bottlenose, *Tursiops truncatus*; rough-toothed, *Steno bredanensis*; and Risso's, *Grampus griseus*, dolphins, and for "blackfish", *Peponocephala electra*/*Feresa attenuata*; pilot whales, *Globicephala macrorhynchus*; and others (Table 4). Among 8 of 10 species-groups specifically identified in Table 4, there were significantly higher percentages of spotted, spinner, and rough-toothed dolphin schools in Area I than in Area II (Fig. 10). Risso's and bottlenose dolphins were important species in both areas, and their percentage values did not differ significantly between the areas. The percentages due to striped and common dolphins and pilot whales increased in Area II relative to Area I. Though reduced, the spotted dolphin remained important in the Area II dolphin community. The increase in percent composition of the common dolphin in Area II was not quite significant, reflecting the inclusion in Area I of that species' distributional lobe off Baja California. Overall, the species composition differed significantly between the two areas, as determined by chi-square contingency test of the frequency of species other than spotted, spinner, striped, and common, i.e., the species not initially considered when delimiting Areas I and II ($\chi^2 = 74.4$, df = 5, $P < 0.005$).

Additional evidence for the distinctiveness of the equatorial and subtropical portions of the Area II community is provided by observations along equatorial transects and transects south and south-

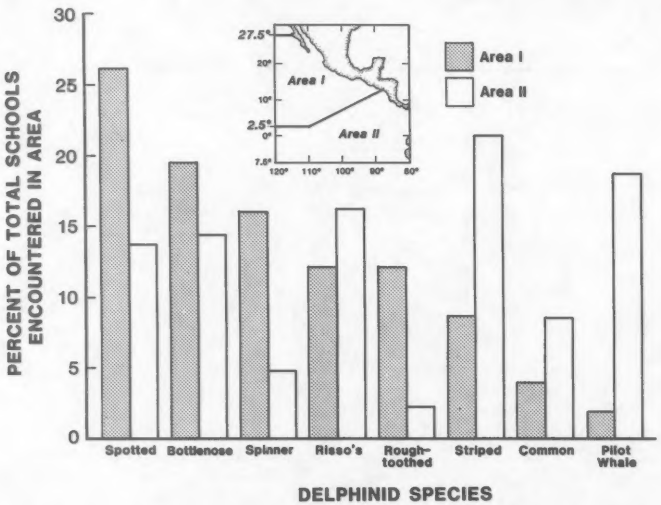

FIGURE 10.—Percent species composition of some important cetaceans, by Area I and II. See Table 4.

TABLE 4.—Percent composition of species as encountered in two areas[1] during the January-March research cruises.

Delphinid spp.[2]	Area I Schools	%	95%[3] C.I.	Area II Schools	%	95%[3] C.I.
Spotted, *Stenella attenuata*	67	24.7	19.6-29.8	55	13.2	10.0-16.4
Spinner, *Stenella longirostris*	41	15.1	10.8-19.4	19	4.6	2.6-6.6
Striped, *Stenella coeruleoalba*	22	8.1	4.9-11.3	86	20.6	16.7-24.5
Common, *Delphinus delphis*	10	3.7	1.5-5.9	34	8.2	5.6-10.8
Pilot whale, *Globicephala macrorhynchus*	5	1.8	0.2-3.4	75	18.0	14.3-21.7
Risso's, *Grampus griseus*	31	11.4	7.6-15.2	65	15.6	12.1-19.5
Bottlenose, *Tursiops truncatus*	50	18.5	13.9-23.1	58	13.9	10.6-17.2
Rough-toothed, *Steno bredanensis*	31	11.4	7.6-15.2	10	2.4	0.9-3.9
"Blackfish", *Peponocephala electra* or *Feresa attenuata*	8	3.0	1.0-5.0	1	0.2	0-0.6
Other	6	2.2	0.2-4.2	14	3.4	1.7-5.1
Total	271			417		

[1]Areas are shown in Figure 10.
[2]Species in mixed schools were tabulated separately.
[3]Normal approximation to binomial distribution.

east of the Galapagos Islands, i.e., off Peru. Unlike during the January-March cruises, physical oceanography was the primary task on most of these transects, hence the ships did not usually divert course toward the schools, and many schools could not be identified. Nevertheless some idea of the species compositions can be obtained. The observations (Table 5) showed that pilot whales and Risso's and bottlenose dolphins were frequently encountered species during October-December off Peru, and common dolphins were often seen near the coast. On the equatorial transects, between long. 85°W and 110°W, striped and common dolphins were the characteristic species. The common dolphin was seen most often near the Galapagos Islands. Pilot whales were relatively abundant during May-July 1981 in this equatorial section. West of long. 110°W along the Equator, pilot whales again were the most frequently encountered species. Interestingly, sightings of Fraser's dolphins, *Lagenodelphis hosei*, and "blackfish" (probably *Peponocephala electra*) were also relatively frequent, especially between long. 110°W and 145°W. These two species often school together and appear to prefer equatorial waters (Perryman et al.[4]). In the next section, another distinctive feature of equatorial waters will be brought out.

Dolphins, Birds, and Tuna

A conspicuous feature distinguishing the dolphin communities is the difference in the species-specific association with tunas. In the eastern tropical Pacific, spinner dolphins and especially spotted dolphins are found associated with "surface" yellowfin tuna. It is these two species, therefore, that are mainly affected by the porpoise-tuna fishery (Smith 1983). Surface tunas occur at the sea surface and can be caught by purse seine, trolling, and pole-and-line gear. "Deep tunas" of the same species are caught by longline gear, generally in and below the thermocline. Since these surface tunas drive food to the surface, making it available to certain seabirds (Ashmole and Ashmole 1957; Murphy and Shomura 1972), a reliable indication that tuna are accompanying a dolphin school is the presence of a bird flock. Birds are the most important cue used by fishermen to locate dolphin-tuna schools.

Birds do not occur equally among the different dolphin species. During the 1977, 1979, and 1980 January-March cruises (when the best bird observa-

[4]Perryman, W. F., D. W. K. Au, and S. Leatherwood. Manuscr. prep. Melon-headed whale, *Peponocephala electra* (Gray, 1946) (with notes on the pygmy killer whale *Feresa attenuata*). Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 5.—Number of schools for species seen a

Dolphin spp.	Region:	Off Peru: 0-10°S, 83°-95°W		Oc
	Ships:	*D. S. Jordan*	*Researcher*	*ogr*
	Dates:	Oct.-Nov. 1977	Oct.-Dec. 1981	Ma 19
Unidentified		7	13	
Spotted, *Stenella attenuata*		3	1	
Spinner, *S. longirostris*		3		
Striped, *S. coeruleoalba*		5	1	
Common, *Delphinus delphis*		4	6	
Bottlenose, *Tursiops truncatus*		10	15	
Pilot, *Globicephala macrorhynchus*		14	9	
Risso's, *Grampus griseus*		23	14	
Rough-toothed, *Steno bredanensis*		1		
Fraser's, *Lagenodelphis hosei*				
"Blackfish", *Peponocephala electra* or *Feresa attenuata*		2		
False killer whale, *Pseudorca crassidens*		1		
Killer whale, *Orsinus orca*		1	1	

seen along equatorial and southeastern Pacific transects.

Equator: 2°N-2°S 85°-110°W			Equator: 2°N-2°S 110°-145°W		Equator: 2°N-2°S 145°-180°W
Ocean-ographer May-July 1981	*Researcher* July-Sept. 1980	*Reseacher* Oct-Dec. 1981	*Ocean-ographer* Mar.-Apr. 1980	*Ocean-ographer* May-July 1981	*Ocean-ographer* Mar.-Apr. 1980
34	20	29	22	8	1
3	3		2	2	1
1	2		1	1	1
14	13	11	3	3	1
18	9	13			
5	4	1		1	
14	4	3	16	5	7
2		1	7		1
1		1	4		1
			7	1	1
1			8		2
		1	1		2
1	2	3			

tions were taken), 70.7% of 167 spotted, spinner, or mixed spotted and spinner dolphin schools, sighted between lat. 5°N and 30°N (where most dolphin-tuna associations occur), had 10 or more associated birds (Table 6). We assume this minimum flock size indicates associated tuna, although we did not often actually see the tuna. For the same period and area, 30.6% of 49 common dolphin schools and only 1.6% of 64 striped dolphin schools were with 10 or more birds. The different percent occurrences indicate that tuna are most frequently associated with spotted and spinner dolphins and very seldom with the striped dolphin.

The bird species most numerous in offshore waters with dolphin schools are boobies (*Sula* spp.); wedge-tailed shearwaters, *Puffinus pacificus*; and sooty terns, *Sterna fuscata*. Frigate birds (*Fregata* spp.) are also closely associated with these dolphins, though their average flock size is only seven (Au and Pitman[5]). These bird species are all strongly dependent upon tunas in their feeding. Our observations are that the birds feed primarily in association with the fish, not the dolphins.

The dolphin-tuna-bird association appears to be area- as well as species-specific. Assuming flocks of ≥10 birds indicate the presence of yellowfin tuna, this association seems to occur in all areas with higher relative abundance of spotted and spinner dolphins (Fig. 11). The association seldom occurs along the Equator, or in areas outside the traditional porpoise-tuna fishing grounds (roughly these are waters within the triangular-shaped area whose base is formed by the American coasts between lat. 25°N and 15°S, and whose apex is at lat. 10°N, long. 150°W; see Calkins 1975 and IATTC 1979-81), even though the required species of dolphins, tuna, and birds may be present there. Relatively few of the spotted or spinner dolphin schools sighted near the Equator were with bird flocks. South of the Equator and in the Central Pacific, there are abundant flocks of sooty terns with fish schools, but dolphins do not usually co-occur (Au and Pitman fn. 5). The most important area of the dolphin-tuna-bird association is centered about the divergence zone near lat. 10°N, an important porpoise-tuna fishing ground for yellowfin tuna (primarily Area I of Figure 10).

These areal changes in the interactions among species are usually clearly apparent during north-south transects across the eastern Pacific during any season. An example is the July-September 1980, NOAA ship *Researcher* transits between Manzanillo, Mexico, and lat. 3°S, long. 100°W, via Clipperton Island. At that time Tropical Surface Water (T > 25°C) extended to the Equator with transition toward Equatorial Water marked by temperature and salinity fronts at lat. 5°N-6°N and at the Equator (Fig. 12). In the tropical waters north of the front at lat. 5°N there was a conspicuous increase in abundance of flocks of sooty terns, boobies, and shearwaters (*Puffinus* spp.), all broadly centered about the thermocline ridge at lat. 10°N. The larger gadfly petrels (*Pterodroma* spp.) were also abundant. All of these birds frequently flock over fish and dolphins. South of this boundary was another avian group, with *Pterodroma leucoptera*, a small petrel from the Southern Hemisphere, and planktivorous storm petrels (*Oceanodroma* spp.) predominating, and peak abundances at the Equator. These latter birds usually feed independently of fish and seldom flock over fish and dolphins.

Correlations among water masses, seabirds, and the different cetaceans along the transect were difficult to quantify because of the small sample size of the latter. However, the observations are supportive of such relationships. There were 39 dolphin schools, of which 15 were unidentified, and 21 whale schools along this transect. Spotted and spinner

[5]Au, D. W. K., and R. L. Pitman. Manuscr. prep. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 6.—Dolphin schools associated with seabirds.

	5°N-30°N			<5°N		
Dolphin spp.	Schools	with ≥10 birds	%	Schools	with ≥10 birds	%
Spotted	95	56	58.9	40	8	20.0
Spotted and spinner	55	53	96.4	21	8	38.1
Spinner	17	9	52.9	19	6	31.6
Common	49	15	30.6	10	1	10.0
Striped	64	1	1.6	76	1	1.3
Rough-toothed	40	5	12.5	13	1	7.7
Other/unidentified	388	17	4.4	189	6	3.2

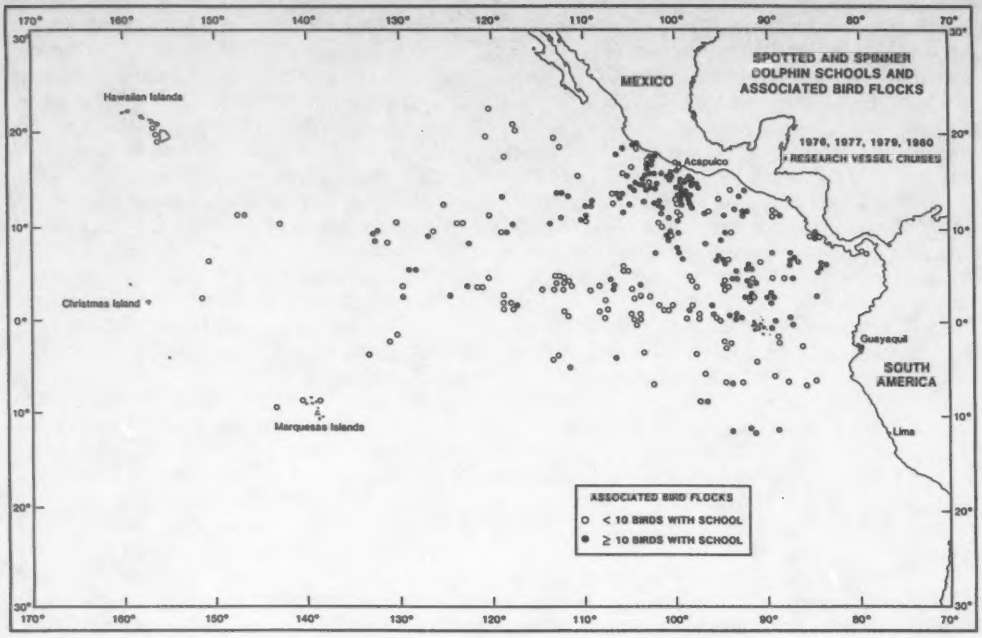

FIGURE 11.—Distribution of bird-associated spotted and spinner dolphin schools during the January-March research cruises. Schools with 10 or more birds are assumed to be with tuna.

dolphns did occur coincidentally with bird flocks (and probably with tuna) in the warmer tropical waters centered about lat. 10°N, but also were seen at the Equator, though without associated bird flocks. Striped and common dolphins occurred in coastal and equatorial waters, without bird flocks. These latter dolphins were the characteristic species on the equatorial transect of this same cruise (see Table 5, col. 4), where only one of the schools seen, a mixed spotted and spinner dolphin school, had an associated bird flock. The distinct change in the bird fauna south of lat. 5°N to species that do not forage commensally with fish suggests there are changes with water masses in the nature of epipelagic prey and how the top predators forage.

DISCUSSION

It should not be surprising that the two major divergence zones of the eastern Pacific, near lat. 10°N and along the Equator, are important features of the oceanic habitats of eastern Pacific cetaceans. Enriched by the effects of wind and the major zonal currents (Brandhorst 1958; Cromwell 1958; Reid 1962; Wyrtki 1966), the zones are evident areas of enhanced biological production (Blackburn 1966, 1976; Blackburn et al. 1970; King 1974; Parsons et al. 1977; Brinton 1979). that are important to tunas (Calkins 1975; Blackburn 1965; Blackburn and Laurs 1972; Blackburn and Williams 1975; Sund 1981) and cetaceans as discussed above. These two zones are not qualitatively the same, however; the strong, shallow thermoclines that have been related to successful porpoise-tuna fishing (Green 1967; Miller et al.[6]) and to aggregations of dolphins and baleen whales (Rovnin 1969; Volkov and Moroz 1976) are characteristic of the lat. 10°N zone, but not of the Equator. Similarly the oxygen minimum layer, noted by Perrin et al. (1976) to be correlated with the distribution of the spotted dolphin, occurs only north and south of the Equator in the eastern Pacific. Equatorial waters are characterized by shallow, weak (<2°C/10 m) thermoclines, due to upwelling and the Equatorial Undercurrent, and cool surface temper-

[6]Miller, F. R., C. J. Orange, R. H. Evans, and K. A. Bliss. Manuscr. prep. Analysis of environment related to tuna fishing in ETP. Inter-American Tropical Tuna Commission, La Jolla, CA 92038.

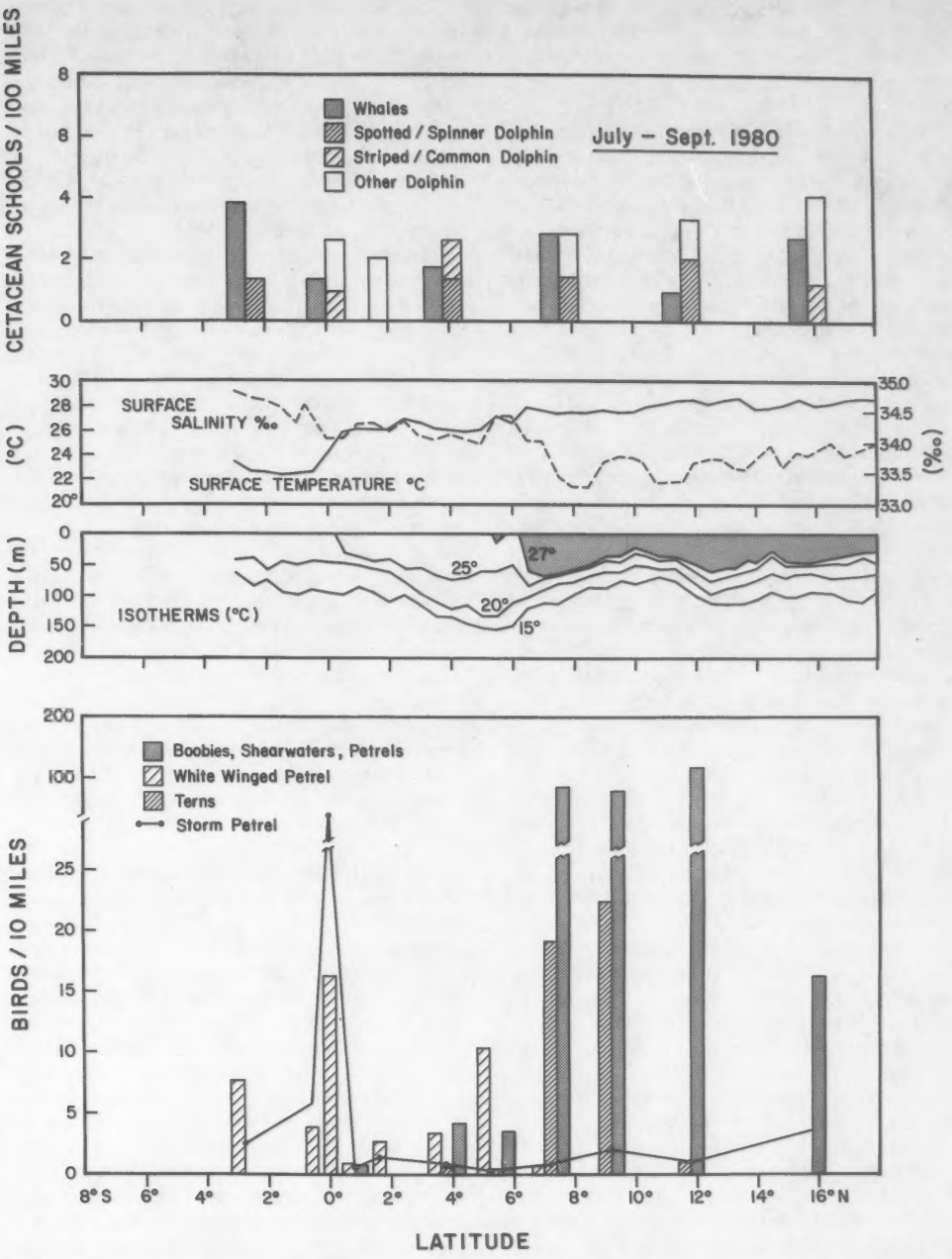

FIGURE 12.—Transect along long. 110°W, July-September 1980, showing changes in cetaceans, birds, and temperature and salinity. The relative abundance of dolphin schools include unidentified schools which were prorated according to species ratios of identified schools.

ature from June through December. These waters support a different cetacean community (Table 5), though school densities there can be as high as in areas off Mexico and Central America (Au et al. 1980).

Other relationships between distribution and movements of dolphins and water masses, convergences, and thermal conditions have been described by Fraser (1934), Gaskin (1968), Kasuya (1971), Nishiwaki (1975), Evans (1975), and Miyazaki and Nishiwaki (1978). Hui (1979) found that common dolphins off California tended to occur over prominent features of bottom topography. The deep depths of such areas suggest that surface eddies and convergences caused by topography-induced accelerations to deep reaching currents (Sverdrup et al. 1942; Neumann 1960) may have concentrated food and attracted the dolphins.

The distributions of dolphin species as seen from the January-March cruises (Figs. 3-7) are similar to the all-season school distributions derived from data of scientific observers aboard tuna seiners. These data, consisting of thousands of sightings per species, were recently summarized by Scott (1981) and Perrin et al. (1983). The same major distributional patterns as presented here for the January-March cruises were apparent, including, for spotted and spinner dolphins, the relative unimportance of equatorial latitudes and the secondary band of increased concentration of schools 2°-5° north of the Equator. The latter may be related to the Equatorial Front and increased food concentration and possibly production in the convergence zone there (Sette 1955; King and Iverson 1962; Blackburn and Laurs 1972; Murphy and Shomura 1972; Pak and Zaneveld 1974; Blackburn and Williams 1975; Greenblatt 1979). Increased abundance of micronekton occurs at least sometime in this zone (Love 1971, 1972; Blackburn and Laurs 1972). The purse seiner data, like those of this paper also showed spotted and spinner dolphins more concentrated in the tropical waters off Mexico and along lat. 10°N, while striped and common dolphins tended to be found in the Central American Bight and along the Equator. This complementary type of distribution was less apparent with the more broadly distributed striped dolphin. It should be noted that our southern distributional lobe for spotted and spinner dolphins, at ca. lat. 5°S, may in part be due to the sampling pattern. However, the density of these dolphins along the Equator is definitely reduced, and we know of no information that does not suggest a rapid decline in density south of our lobe.

Our January-March data differs from the all-season data in indicating fewer schools in the area around the Revilla Gigedo Islands (at ca. lat. 19°N, long. 111°W) and between long. 90°W and 100°W along lat. 10°N for spotted and spinner dolphins. Also our data suggested that striped and common dolphins had a more localized distribution near the region of the Costa Rica Dome, and were relatively infrequent between long. 105°W and 120°W, along lat. 10°N. These differences may be due to seasonal changes in distribution.

The relative densities of these dolphins, as school encounter rates in the tuna purse seine fishery, were recently calculated by Polacheck (1983). The patterns he derived were fragmentary, but not inconsistent with those of this paper. He showed, for example, higher densities of spotted and spinner dolphins extending to the southwest from off southern Mexico and reduced densities in the Central American Bight. For striped and common dolphins, he also described a three-lobed distribution pattern as in this paper. However his equatorial lobe was centered just south of the Equator.

It seems likely that the dolphin community of the Upwelling-Modified Water differs from the Tropical Water community because of water-mass specific differences in the distribution and availability of food. This is supported by the different biotic features of Equatorial and Subtropical Waters relative to Tropical Waters. The distinction is clearly shown by the surface distribution of nutrients and primary production in these waters as measured during the EASTROPAC cruises (Love 1971, 1972). The equatorial waters of the eastern Pacific in particular are different. They support abundant plankton-feeding storm petrels rather than fish and cephalopod-feeding flocking birds that are usually abundant both north and south of the Equator (see also Love 1971, 1972 and King 1974). Dolphin species along the Equator tend not to be with fish or birds (Figs. 11, 12), and the species composition of the cetacean community appears to be distinct (Table 5; Au and Pitman 1981). Of course it has previously been known that equatorial waters are notable in being important sperm whale grounds (Townsend 1935) and have a zooplankton community distinct from other parts of the eastern tropical Pacific (McGowan 1972). Finally the fact that the common dolphin, a species characteristic of coastal upwelling waters from California to Peru, occurs with greater frequency in the equatorial waters and near upwelling areas in the Central American Bight, suggests that the shorter and different food chains of the upwelling environments (Parsons et al. 1977) may be the basis of the community difference.

The dolphin-tuna-bird association is one manifestation of community difference that is both striking and of ecological interest. The distribution of this association is notable in that it seems coincident with both the main habitats of spotted and spinner dolphins and the distribution of "surface" yellowfin tuna in the eastern Pacific (see Figure 11, Shingu et al. 1974, and Suzuki et al. 1978). Since it is primarily these dolphins that are associated with birds and with yellowfin tuna, the geography of the dolphin-bird association also defines that of the dolphin-yellowfin tuna association. This association of birds and fish with dolphins occurs in all tropical waters, including the southern Subtropical Water during the southern summer. It is apparently rare in equatorial waters of the eastern Pacific, in the central and western Pacific (Myazaki and Wada 1978; Au et al. fn. 2), and in the eastern tropical Atlantic (Levenez et al. 1980). In the central Pacific the same bird species found with spotted and spinner dolphins in the eastern tropical Pacific can be abundant (Gould 1974), and sooty terns especially, are frequently associated with small tunas, but these are most likely skipjack tuna (Murphy and Ikehara 1955; Waldrom 1964; Hida 1970; Blackburn and William 1975). Apparently those flocks seldom accompany dolphins or schools of larger yellowfin tuna. Yellowfin tuna and dolphins seldom seem to associate outside the eastern tropical Pacific.

The obvious feeding activity often seen in these joint aggregations of birds, spotted and spinner dolphins, and tuna suggests that these species have similar food and foraging requirements. Our observations indicate that the mammals and fish are not tightly associated in the aggregations (see Au and Perryman 1982) and probably feed independently (see also Norris and Dohl 1980a). However the tuna, birds, and spotted dolphin (at least) do appear to be feeding at the same time. Both the tuna and spotted dolphins feed on epipelagic fish and on squids (Perrin et al. 1973; Olson 1982), but the spinner dolphins feed differently and may forage more at night (Perrin et al. 1973; Norris and Dohl 1980b); though they are active in these feeding aggregations, they may not be directly associated with the tuna. Judging from the associations of bird and dolphin species, only spotted and spinner dolphins frequently find it advantageous to feed with yellowfin tuna. Furthermore the distribution of this association suggests that the necessary kind and behavior of prey that is likely the basis of the association appears characteristic of tropical, but not equatorial, waters. It occurs especially where a shallow thermocline may constrain the yellowfin tuna to the surface layer with the dolphins, a complex interaction between environment and physiology (Sharp 1978) that may cause the phenomenon known as "surface tuna". Finally the distribution of the bird-dolphin association indicates that the dolphin-tuna association is characteristic of areas of higher school density of spotted and spinner dolphins. High population densities of both dolphins and yellowfin tuna, and suitable prey are therefore likely requisites for joint dolphin-tuna schools. The dolphin-tuna association is a feature of the most productive tuna fishing zones of these tropical seas. In such rich areas, feeding tactics to exploit clumped prey could lead to multispecies aggregations of predators, as explained by Schoener (1982).

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LITERATURE CITED

ALVERSON, F. G.
1981. Comments on the distribution of spotted, spinner, common and striped dolphin in the tropical Pacific Ocean. *In* P. S. Hammond (editor), Report on the Workshop on Tuna-Dolphin Interactions, p. 109-124. Inter-Am. Trop. Tuna Comm., Spec. Rep. 4, App. 5.

ASHMOLE, N. P., AND M. J. ASHMOLE.
1957. Comparative feeding ecology of seabirds of a tropical oceanic island. Yale Univ. Peabody Mus. Nat. Hist. Bull. 24:1-131.

AU, D. W., W. L. PERRYMAN, R. L. PITMAN, AND M. S. SINCLAIR.
1980. Cetacean populations and equatorial oceanography. Trop. Ocean Atmos. Newsl., Univ. Wash., 4:6-10.

AU, D. W. K., AND R. L. PITMAN.
1981. The equatorial cetacean community of the eastern Pacific. (Abstr.) Proceedings of the Fourth Biennial Conference on the Biology of Marine Mammals, Dec. 14-18, 1981, p. 95.

AU, D., AND W. PERRYMAN.
1982. Movement and speed of dolphin schools responding to an approaching ship. Fish. Bull., U.S. 80:371-379.

BENNETT, E. B.
1966. Monthly charts of surface salinity in the eastern tropical Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 11:3-44.

BLACKBURN, M.
1965. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol. Annu. Rev. 3:299-322.
1966. Biological oceanography of the eastern tropical Pacific: summary of existing information. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 540, 18 p.
1976. Review of existing information on fishes in the deep ocean mining environment study (DOMES) area of the tropical Pacific. Inst. Mar. Res., Univ. Calif., IMR NO. 76-1, 77 p.

BLACKBURN, M., AND R. M. LAURS.
1972. Distribution of forage of skipjack tuna (*Euthynnus pelamis*) in the eastern tropical Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-649, 16 p.

BLACKBURN, M., R. M. LAURS, R. S. OWEN, AND B. ZEITSCHEL.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton, and micronekton in the eastern tropical Pacific. Mar. Biol. (Berl.) 7:14-31.

BLACKBURN, M., AND F. WILLIAMS.
1975. Distribution and ecology of skipjack tuna, *Katsuwonus pelamis*, in an offshore area of the eastern tropical Pacific Ocean. Fish. Bull., U.S. 73:382-411.

BRANDHORST, W.
1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. J. Cons. Int. Explor. Mer 24:16-31.

BRINTON, E.
1979. Parameters relating to the distribution of planktonic organisms, especially euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8:125-189.

CALKINS, T. P.
1975. Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971-1974. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 17:3-116.

CROMWELL, T.
1958. Thermocline topography, horizontal currents and "ridging" in the eastern tropical Pacific. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 3:135-164.

EVANS, W. E.
1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. Thesis, Univ. California, Los Angeles, 164 p.

FORSBERGH, E. D.
1969. On the climatology, oceanography, and fisheries of the Panama Bight. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 14:45-385.

FRASER, F. C.
1934. Report on cetacea stranded in British coasts from 1927 to 1932. Br. Mus. (Nat. Hist.) No. 11, 41 p.

GASKIN, D. E.
1968. Distribution of delphinidae (Cetacea) in relation to sea surface temperature off eastern and southern New Zealand. N.Z. J. Mar. Freshw. Res. 2:527-534.

GOULD, P. J.
1974. Sooty tern (*Sterna fuscata*). *In* W. B. King (editor), Pelagic studies of seabirds in the central and eastern Pacific Ocean, p. 6-52. Smithson. Contrib. Zool. No. 158.

GREEN, R. E.
1967. Relationship of the thermocline to success of purse seining for tuna. Trans. Am. Fish. Soc. 96:126-130.

GREENBLATT, P. R.
1979. Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull., U.S. 77:147-155.

HIDA, T. S.
1970. Surface tuna schools located and fished in equatorial eastern Pacific. Commer. Fish. Rev. 32(4):34-37.

HOFMANN, E. E., A. J. BUSALACCHI, AND J. J. O'BRIEN.
1981. Wind generation of the Costa Rica Dome. Science (Wash., D.C.) 214:552-554.

HUI, C. A.
1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. J. Mammal. 60:521-527.

INTER-AMERICAN TROPICAL TUNA COMMISSION.
1979. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.
1980. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.
1981. Annual report of the Inter-American Tropical Tuna Commission. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, CA.

KASUYA, T.
1971. Consideration of distribution and migration of toothed whales of the Pacific coast of Japan based upon aerial sighting record. Sci. Rep. Whales Res. Inst. 23:37-60.

KING, J. E., AND R. T. B. IVERSON.
1962. Midwater trawling for forage organisms in the central Pacific 1951-1956. U.S. Fish Wildl. Serv., Fish. Bull. 62: 271-321.

KING, W. B. (editor).
1974. Pelagic studies of seabirds in the central and eastern Pacific Ocean. Smithson. Contrib. Zool. No. 158, 277 p.

LEVENEZ, J., A. FONTENEAU, AND R. REGALADO.
1980. Resultats d'une enquete sur l'importance des dauphins dans la pecherie thoniere FISM. Int. Comm. Conserv. Atl. Tunas, Coll. Vol. Sci. Pap. IX(1):176-179.

LOVE, C. M. (editor).
1971. Biological and nutrient chemistry data from principal participating ships, first survey cruise, February-March 1967. EASTROPAC Atlas, Vol. 2. Natl. Mar. Fish. Serv., Circ. 330, 87 p.
1972. Biological and nutrient chemistry data from principal participating ships, second survey cruise, August-September 1967. EASTROPAC Atlas, Vol. 6. Natl. Mar. Fish. Serv., Circ. 330, 80 p.

MCGOWAN, J. A.
1972. The nature of oceanic ecosystems. *In* C. B. Miller (editor), The biology of the oceanic Pacific, p. 9-28. Proc. 33d Annu. Biol. Colloq., Oreg. State Univ. Press, Corvallis, OR.

MIYAZAKI, N., AND M. NISHIWAKI.
1978. School structure of the striped dolphin off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. 30:65-115.

MIYAZAKI, N., AND S. WADA.
1978. Observations of cetacea during whale marking cruise in the western tropical Pacific 1976. Sci. Rep. Whales Res. Inst. 30:179-195.

MURPHY, G. I., AND I. I. IKEHARA.
1955. A summary of sightings of fish schools and bird flocks and of trolling in the central Pacific. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 154, 19 p.

MURPHY, G. I., AND R. S. SHOMURA.
1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull., U.S. 70:875-913.

NEUMANN, G.
1960. On the effect of bottom topography on ocean currents. Dtsch. Hydrogr. Z., 13:132-141.

NISHIWAKI, M.
1975. Ecological aspects of smaller cetaceans, with emphasis on the striped dolphin (*Stenella coeruleoalba*). J. Fish. Res. Board Can. 32:1069-1072.

NORRIS, K. S., AND T. D. DOHL.
1980a. The structure and functions of cetacean schools. *In* L. M. Herman (editor), Cetacean behavior, mechanisms and functions, p. 211-261. John Wiley and Sons, N.Y.
1980b. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish. Bull., U.S. 77:821-849.

OLSON, R. J.
1982. Feeding and energetic studies of yellowfin tuna, food for ecological thought. Coll. Vol. Sci. Pap., Int. Comm. Conserv. Atl. Tunas XVII(2):444-457.

PARSONS, T. R., M. TAKAHASHI, AND M. HARGRAVE.
1977. Biological oceanographic processes. Pergamon Press, N.Y., 332 p.

PAK, H., AND J. R. V. ZANEVELD.
1974. Equatorial front in the eastern Pacific Ocean. J. Phys. Oceanogr. 4:570-578.

PERRIN, W. F.
1975a. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board Can. 32:1059-1067.
1975b. Variation of the spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. 21, 206 p.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

PERRIN, W. F., D. B. HOLTS, AND R. B. MILLER.
1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725-750.

PERRIN, W. F., G. J. WALKER, F. M. RALSTON, AND D. W. K. AU.
1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific with an annotated catalog of data sources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-38, 65 p.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

POLACHECK, T.
1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph.D. Thesis, Univ. Oregon, Eugene, 475 p.

REID, J. L., JR.
1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287-306.

ROVNIN, A. A.
1969. Distribution of true whales in the tropical part of the Pacific. *In* V. A. Arseniev, B. A. Zenkovich, K. K. Chapsky (editors), Transactions of the Third All-Union Conference on Marine Mammals, p. 144-149. Nauka, Moskva, U.S.S.R.

SCHOENER, T. W.
1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

SCOTT, M. D.
1981. Dolphin stocks in the eastern tropical Pacific. *In* P. S. Hammond (editor), Report on the workshop on tuna-dolphin interactions, p. 98-107. Inter-Am. Trop. Tuna Comm. Spec. Rep. No. 4, App. 4.

SETTE, O. E.
1955. Consideration of midocean fish production as related to oceanic circulatory systems. J. Mar. Res. 14:398-414.

SHARP, G. D.
1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 397-449. Acad. Press, N.Y.

SHINGU, C., P. K. TOMLINSON, AND C. L. PETERSON.
1974. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1967-1970. [In Engl. and Span.] Bull. Inter-Am. Trop. Tuna Comm. 16:67-230.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull., U.S. 81:1-13.

SUND, P. N., M. BLACKBURN, AND F. WILLIAMS.
1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Annu. Rev. 19:443-512.

SUZUKI, Z., P. K. TOMLINSON, AND M. HONMA.
1978. Population structure of Pacific yellowfin tuna. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm. Bull., 17:277-358.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans, their physics, chemistry, and general biology. Prentice-Hall, Inc., N.Y., 1087 p.

TOWNSEND, C. H.
1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19:1-50.

VOLKOV, A. F., AND I. F. MOROZ.
1976. Oceanological conditions of the distribution of cetacea in the eastern tropical part of the Pacific Ocean. Int. Whaling Comm. Rep. 27:186-188.

WALDRON, K. D.
1964. Fish schools and bird flocks in the central Pacific Ocean, 1950-1961. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 464, 20 p.

WYRTKI, K.
1964a. The thermal structure of the eastern Pacific Ocean. Erganzungsh. Dtsch. Hydrogr. Z. Reiche A 8(6), 84 p.
1964b. Upwelling in the Costa Rica Dome. U.S. Fish Wildl. Serv., Fish. Bull., 63:355-372.
1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev. 4:36-68.
1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117-147.
1974. Equatorial currents in the Pacific 1950 to 1970 and their relations to the trade winds. J. Phys. Oceanogr. 4:372-380.

ASPECTS OF THE LIFE HISTORY OF THE FLUFFY SCULPIN, *OLIGOCOTTUS SNYDERI*

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ABSTRACT

We examined age structure, growth rates, and diets of male and female *Oligocottus snyderi* Greeley at Dillon Beach, CA, where this sculpin numerically dominates the mid- and lower intertidal fish assemblage. Two age classes, 0+ and 1+, were present; maximum lifespan was about 1.5 years. Instantaneous population growth rates were highest for the 0+ age class, and most individuals attained spawning size during the first year of life. Growth rates for both age classes were highest during the high productivity Upwelling period and minimal during the low productivity, Oceanic-Davidson Current period.

Males and females primarily consumed gammarid amphipods and polychaetes. Larger individuals (≥50 mm SL) of both sexes consumed a wider variety of prey, including shrimps, crabs, and isopods. Among year and seasonal dietary changes were minimal. Females consumed two times more gammarids by weight than males during the low productivity Oceanic-Davidson Current period, when ovarian recrudescence occurs. Females may increase food consumption to meet the increased energetic demands of egg production.

Rapid sexual maturation and growth and the occurrence of recruitment during upwelling probably are adaptations to the pronounced annual cycle of productivity. These adaptations, together with intense utilization of an abundant prey (gammarids) not widely consumed by other assemblage members, probably contribute to *O. snyderi*'s numerical dominance in the rocky intertidal of central California.

The fluffy sculpin, *Oligocottus snyderi* Greeley, is a common species which inhabits the rocky intertidal from Baja California to Sitka, AK (Miller and Lea 1972). Between central California and British Columbia, *O. snyderi* frequently is very abundant (Green 1971; Cross 1981; Yoshiyama 1981; Grossman 1982). This species occurs primarily in mid- and lower intertidal areas (Green 1971; Yoshiyama 1981), and often is associated with surfgrass (Green 1971; Nakamura 1976a). The general absence of this species from the high intertidal is probably due to its inability to tolerate higher temperatures which frequently occur in high intertidal pools (Nakamura 1976b).

Life histories of intertidal fishes, particularly cottids, are poorly known (Gibson 1969, 1982). Published information on the demography of *O. snyderi* is restricted to the work of Moring (1981), who examined age structure of a northern California *O. snyderi* population, and Grossman and deVlaming (1984), who described the species' reproductive ecology. This paper presents data on age structure, growth rates, and dietary habits of an *O. snyderi* population at Dillon Beach, CA, a site that is subject to pronounced annual cycles of oceanic productivity (Parrish et al. 1981). *Oligocottus snyderi* numerically dominates the intertidal fish assemblage at Dillon Beach (Grossman 1982); the present study explores demographic and ecological characteristics which may account for this species' ecological success in the rocky intertidal.

MATERIALS AND METHODS

Collections

Oligocottus snyderi were collected from a series of mid- and lower intertidal pools at Dillon Beach, CA, on 15 dates from January 1979 to July 1981 (see Grossman in press a for sampling dates). Repeated collecting did not affect assemblage structure (Grossman 1982, in press a). Fish were obtained by spreading a 10% solution of quinaldine in isopropanol through the pools and then collecting individuals after anesthetization. Over 1,400 *O. snyderi* were collected. Specimens were preserved in buffered Formalin[3] and were later washed and transferred to 45% isopropanol. Individuals were measured to the nearest millimeter standard length (SL) and weighed to the nearest 0.1 g. Sexes of all

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individuals collected during 1979 and of specimens used for gut analysis also were recorded. A complete description of collecting methods and the study site are presented in Grossman (1982, in press b).

Collection dates were assigned either to the Upwelling or the combined Oceanic-Davidson Current (ODC) oceanographic seasons, based on water temperature and a calculated upwelling index (see Grossman in press b). The Upwelling period is characterized by frequent upwelling of nutrient-rich waters and high productivity (Bolin and Abbott 1963; Garrison 1979). In contrast, the ODC period exhibits minimal upwelling, frequent downwelling, and low productivity (Bolin and Abbott 1963; Garrison 1979). Data from individuals collected during the latter seasons were pooled because these periods were not readily distinguishable (Grossman in press b). Consequently, comparisons of *O. snyderi* food habits and length-weight relationships represent contrasts between a high productivity period (Upwelling, all months from April to August, plus March 1980) and the low productivity ODC period (October-February, plus March 1979). Monthly mean water temperatures ranged from 9.7° to 11.9°C during the Upwelling period from 11.2° to 14.2°C during the ODC period (Grossman in press b).

Length-Weight and Growth Calculations

Regressions of individual weight versus standard length were calculated separately for males and females collected in the Upwelling and ODC periods. Regression equations were of the form $W = aL^b$, fitted as $\ln W = \ln a + b \ln L$. Slopes (b) of regression equations for males and females were compared for each period by analysis of covariance (ANCOVA). Seasonal differences between slopes also were examined for each sex.

Regression slopes for the two sexes and periods were divided by their correlation coefficients to estimate slopes for geometric mean functional regressions of weight versus length (Ricker 1973). Functional regressions are recommended for describing relations between weight and length because both variables are subject to natural variability (Ricker 1973). Functional regression slopes were used to derive y-intercepts from the equation $y\text{-int.} = \bar{y} - (b/r)\bar{x}$ (Ricker 1973). These slope estimates were employed to calculate instantaneous rates of growth in weight (G) as

$$G = (b/r)(\ln L_2 - \ln L_1), \text{ (Ricker 1975),}$$

where b/r = slope of the functional length-weight regression;
L_1 = mean length at the time t; and
L_2 = mean length at time $t + 1$.

Growth rates were calculated for individual year classes which were separated using length-frequency distributions. To compare growth rates for males and females, t-tests for paired samples were used.

Sex ratios for the 1979 samples were tested for deviations from unity using chi-square tests corrected for continuity.

Dietary Analyses

Stomach contents were removed from a subsample (597 total) of the *O. snyderi* collected between January 1979 and July 1981. Ninety-seven percent of stomachs examined contained food. Prey were identified to the lowest possible taxon and weighed (wet) to the nearest milligram. The weights of each prey type were pooled separately for males and females from each collection. Diets were then calculated as the percent of the total stomach content weight attributable to each prey type. The number of fish containing each prey type (i.e., prey frequency of occurrence, henceforth FO) also was recorded.

Dietary data were pooled across collections within the Upwelling and ODC periods for each sex, to compare feeding habits between sexes and seasons. Because the study period spanned 3 yr, it also was possible to quantify among year variability in seasonal and sex-specific feeding habits. Sex-linked ontogenetic dietary changes were examined by separating males and females into 20 mm size classes and comparing prey consumed by each size class in different seasons and years. Niche breadth was calculated as $\Sigma\ 1/p_i^2$ (Levins 1968), where p_i is the proportion of the total prey weight comprised of the ith prey type. Only prey types constituting at least 1% of the total prey weight were included in niche breadth calculations. Niche breadth was compared among size classes by using the Wilcoxon signed-rank test.

RESULTS

Length-Weight Relationships

The slope for the male length-weight regression for the Upwelling period was significantly greater than that for females (ANCOVA, $F = 12.875$, $P < 0.001$; Table 1). Slopes of length-weight regressions for males and females collected during the ODC period were not significantly different (ANCOVA,

TABLE 1.—Length-weight relationships, described as $W = aL^b$, for *Oligocottus snyderi*. Coefficients for the least-squares (ln W = ln a + b ln L) and functional (ln W = ln a' + (b/r) ln L) regressions are presented, as well as the correlation coefficients for the least-squares regressions (r) and the number of individuals used in each regression (N). ODC = Oceanic-Davidson Current.

			Least-squares regression		Functional regression	
	N	r	a	b	a'	b/r
Males						
Upwelling	150	0.984	0.0000178	3.097	0.0000146	3.147
ODC	112	0.973	0.0000253	2.991	0.0000182	3.075
Females						
Upwelling	164	0.972	0.0000472	2.835	0.0000346	2.917
ODC	131	0.976	0.0000202	3.069	0.0000151	3.143

$F = 0.736, P > 0.25$). Seasonal comparisons for each sex showed that the male Upwelling and ODC slopes were not significantly different (ANCOVA, $F = 1.483$, $P > 0.10$), whereas the females had a significantly higher slope during the ODC period (ANCOVA, $F = 6.147$, $P < 0.025$).

Growth Rates

Length-frequency histograms for *O. snyderi* at Dillon Beach indicated that two year classes were present on most dates (Fig. 1). Recruitment began in spring and peaked during summer. The onset of recruitment differed between years. Age 0+ fish were first taken in May of 1979; however, in 1980 recruitment began in March. Age 0+ individuals of the 1979 cohort grew 20 mm in length (from 20-25 to 40-55 mm SL) by December of their first year. Members of the 1978 cohort (= age 1+ fish) increased in length from 40-55 to 60-70 mm SL during spring, summer, and fall 1979. Individuals did not appear to survive a second winter during 1980, although a few males recruited in 1977 may have survived until spring of 1979 (Fig. 1).

Sex ratios for the 0+ age class were significantly different from unity in the August 1979 collection in which there were significantly more males than females (1.7:1; $\chi^2 = 7.32$, $P < 0.01$). Age 1+ females significantly outnumbered males in January 1979 (4:1; $\chi^2 = 6.05$, $P < 0.025$), July 1979 (1.8:1; $\chi^2 = 4.38$, $P < 0.05$), and December 1979 (3:1; $\chi^2 = 5.04$, $P < 0.025$).

Instantaneous growth rates were calculated for males and females from the two year classes present in 1979 (Table 2). Prolonged recruitment (lasting from May through August) resulted in apparent depressed spring and summer growth rates for the age 0+ class when all individuals were included in the calculations of mean lengths (Table 2). Therefore, fish which appeared to have been recruited later than the majority of the class were excluded from consideration in the June, July, and August calculations, as shown in Figure 1. Only the very large males collected in January 1979 were excluded from the age 1+ mean length calculations, as these individuals apparently were survivors from the 1977 year class and probably died shortly thereafter. The highest monthly instantaneous growth rates were obtained during May and June, averaging 0.860 and 0.655 for age 0+ males and females, and 0.209 and 0.188 for age 1+ males and females (Table 2, Fig. 2). Growth rates markedly decreased after August, averaging 0.065 and 0.169 for age 0+ males and females, and 0 and 0.061 for age 1+ males and females during October and November (Table 2, Fig. 2).

Males and females attained nearly equal lengths in the first season of growth; however, age 1+ males displayed significantly greater mean lengths (t-tests, $P << 0.05$) than age 1+ females from June through November 1979 (Fig. 2). Growth rates were not significantly higher for males than females in either size class when compared from January to December 1979 (age 0+: $t = 1.002$, $P > 0.1$; age 1+: $t = 1.232$, $P > 0.1$); however, if only the data from January to October are included for the age 1+ class, males did have significantly higher growth rates ($t = 2.255$, $P < 0.05$). This discrepancy is caused by the low numbers of age 1+ fish collected in November (14) and December (24). Length-frequency histograms (Fig. 1) also show that age 1+ males are larger than females, whereas length distributions are

TABLE 2.—Instantaneous growth rates of *Oligocottus snyderi* males and females in their first (age 0+) and second (age 1+) years of growth. Rates were calculated for the intervals between the 1979 collections. Values in parentheses were calculated with all individuals included in the age 0+ cohort (see text).

Collection dates	Instantaneous growth rate			
	Age 0+		Age 1+	
	Males	Females	Males	Females
1-27-79				
	—	—	0.257	0.079
3-26-79				
	—	—	0.295	0.171
5-16-79				
	1.059 (1.059)	0.718 (0.562)	0.318	0.204
6-13-79				
	0.661 (0.429)	0.591 (0.358)	0.099	0.171
7-12-79				
	0.352 (0.306)	0.295 (0.390)	0.111	0.074
8-09-79				
	0.303 (0.582)	0.124 (0.419)	0.164	0.063
10-07-79				
	0.129	0.149	0	0.122
11-04-79				
	—	0.188	—	—
12-04-79				

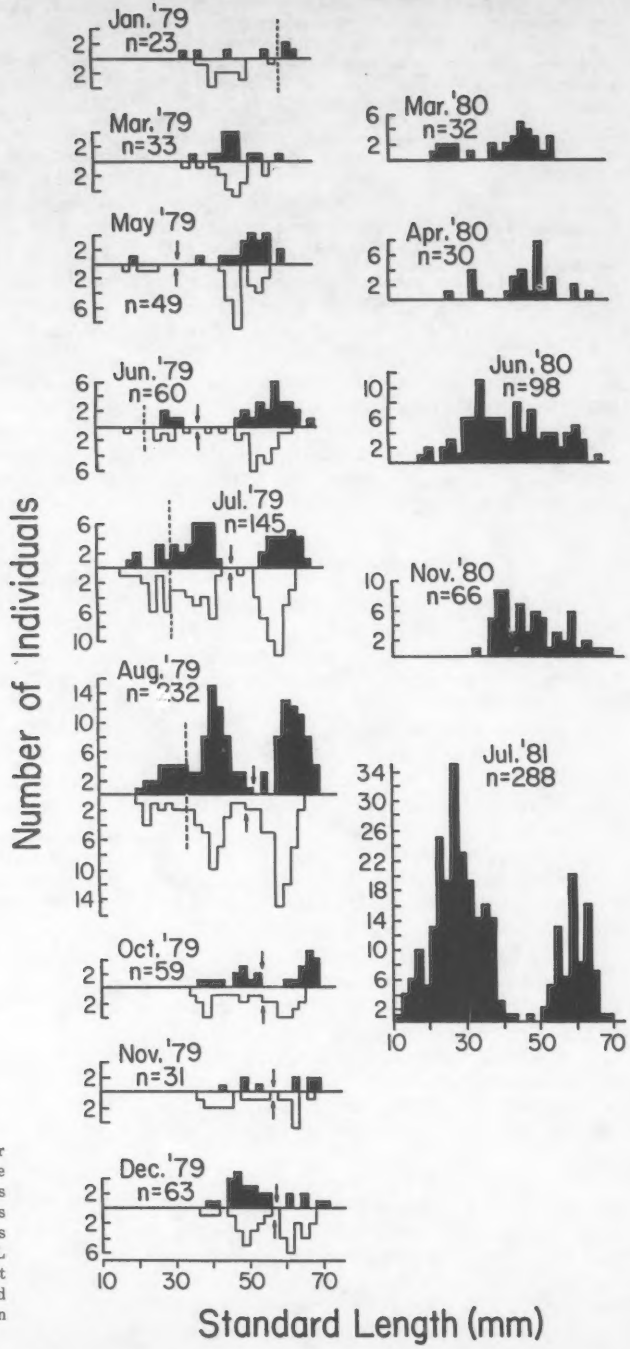

FIGURE 1.—Length-frequency distributions for *Oligocottus snyderi*. Males and females are separated in the 1979 collections, with females shown below the axis. Arrows indicate divisions between year classes 0+ and 1+, and broken lines designate limits for inclusion in cohort mean SL calculations (January, June, July, and August 1979). The 1980 and 1981 collections are included for comparison, but the sexes are not shown separately.

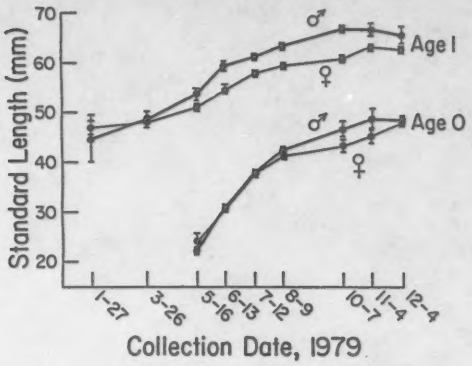

FIGURE 2.—Growth curves for age 0+ and 1+ *Oligocottus snyderi*. The standard lengths ($\bar{x} \pm$ SE) of each sex in the two age classes are shown for the 1979 collections. June, July, and August age 0+ SLs do not include late recruited individuals (see text and Figure 1).

about equal for age 0+ males and females. The low mean lengths calculated for age 0+ females in October and November resulted from the inclusion of small individuals probably recruited late in Upwelling, but which were not easily separable from the remainder of the cohort. Hence, calculated growth rates probably underestimate age 0+ female growth from August to October and overestimate growth from October to December.

Dietary Habits

Oligocottus synderi's diet at Dillon Beach consisted primarily of gammarid amphipods and polychaetes. Summed across all collections, gammarids composed 78% and 66% of the gut contents of females and males, respectively. Polychaetes totaled 10% of the female diet and 14% of the male diet. Shrimp remains, mainly *Heptacarpus taylori*, contributed 5% and 4% to female and male diets, respectively. A total of 20 prey taxa were consumed by *O. snyderi*; however, no other prey category composed more than 3% of the diet, with the exception of unidentifiable hard-bodied prey remains, which totaled 5% of the gut contents of males. Dietary breadth based on all collections was higher for males than females (2.17 vs. 1.61), because males consumed greater amounts of minor prey types.

The major seasonal dietary changes for both males and females were decreased gammarid consumption and increased polychaete consumption during Upwelling as compared with the ODC period (Tables 3, 4). Dietary breadth also was greater for both sexes during Upwelling than in the ODC period (2.02 vs. 1.44 for females, and 2.19 vs. 2.09 for males). Differences were observed between male and female diets. Specifically, in the ODC period, gammarids composed a greater proportion of female than male diets (83% vs. 68%), whereas males consumed proportionately more eggs, *Idotea* spp. (Isopoda), and crabs (Table 4). Although standard lengths and weights of ODC males (138) and females (132) used for gut analyses were not significantly different (SL: $t = 1.058$, $P > 0.1$; weight: $t = 1.036$, $P > 0.1$), females had significantly greater amounts of food in their stomachs ($t = 4.857$, $P = 0.0001$, Table 4). This difference is attributable to the weight of ingested gammarids because 131 (FO) females contained a total of 8.4 g of gammarids, whereas 132 males contained only 4.3 g (total weight).

Examination of food habits across size classes shows that larger individuals generally possessed a more diverse diet than smaller individuals (Figs. 3, 4). Dietary breadth was significantly higher (Wilcoxon signed-rank test, $n = 12$, $T = 69$, $P < 0.01$) for 50-69 mm SL fish than for 30-49 mm SL individuals when compared across both sexes for all years. Individuals <30 mm SL consumed mainly gammarids and isopods; polychaetes and shrimp were major prey only for larger fish. *Pagurus* spp. and crabs, including *Cancer* spp. and *Pachycheles* spp., were found only in individuals ≥40 mm SL.

The general observation of decreased gammarid consumption by larger *O. snyderi*, concomitant with increased polychaete and shrimp consumption, applies to collections made throughout the 3-yr study period. The majority of among year variation in food habits resulted from the presence of large, rare prey items in single individuals (Figs. 3, 4). An exception was the high consumption of polychaetes by males collected in July 1981 (Fig. 3). In this case, polychaetes occurred in all of the 50-69 mm fish and in 56% of the 30-49 mm fish, and composed a considerably higher proportion of the diet than during previous Upwelling collections.

DISCUSSION

Age-Structure and Growth

At Dillon Beach, a habitat displaying marked seasonal fluctuations in productivity (Grossman 1982, in press b; Grossman and deVlaming 1984), *O. snyderi* is short lived, with a maximum lifespan of about 1.5 yr and a maximum length of about 70 mm SL. Whereas two age classes were observed in this study, Moring (1981) observed as many as three age classes in Trinidad Bay. Standard lengths attained

TABLE 3.—Food habits of male and female *Oligocottus snyderi* collected during the Upwelling period. Values shown for each prey type are total weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, n = 164 45.9 ± 11.7 mm			Males, n = 150 51.3 ± 11.8 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	3.850	68	(125)	3.653	64	(132)
Polychaetes	0.980	17	(19)	1.109	19	(33)
Heptacarpus taylori	0.202	4	(4)	0.222	4	(5)
Crangon	0.146	3	(2)	0		
Other shrimp	0.001	<1	(1)	0.004	<1	(1)
Hard-bodied prey rem.	0.196	3	(18)	0.494	9	(20)
Isopods	0.095	2	(10)	0.074	1	(19)
Idotea	0.006	<1	(2)	0.049	1	(3)
Pagurus	0.067	1	(1)	0		
Crabs	0.036	1	(2)	0.026	<1	(1)
Algae	0			0.039	1	(9)
Snails	0.024	<1	(4)	0.010	<1	(3)
Caprellids	0.026	<1	(1)	0.004	<1	(2)
Soft-bodied prey rem.	0			0.014	<1	(1)
Barnacle cirri	0			0.012	<1	(5)
Total	5.629	99		5.710	99	

TABLE 4.—*Oligocottus snyderi* feeding habits during the combined Oceanic-Davidson Current periods. Values shown for each prey are the weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, n = 132 49.5 ± 8.8 mm			Males, n = 138 50.6 ± 9.3 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	8.418	83	(131)	4.278	68	(132)
Polychaetes	0.611	6	(20)	0.587	9	(23)
Heptacarpus taylori	0.304	3	(3)	0.308	5	(4)
Crangon	0.089	1	(2)	0		
Other shrimp	0.071	1	(1)	0		
Eggs	0.008	<1	(1)	0.397	6	(6)
Idotea	0.131	1	(6)	0.252	4	(14)
Isopods	0.255	3	(19)	0.104	2	(16)
Sea anemones	0.147	1	(2)	0		
Hard-bodied prey rem.	0.053	1	(2)	0.086	1	(4)
Pachycheles	0			0.091	2	(1)
Barnacle cirri	0.001	<1	(1)	0.075	1	(5)
Pagurus	0.043	<1	(2)	0		
Bivalves	0			0.036	1	(1)
Algae	0			0.044	1	(9)
Caprellids	0.015	<1	(2)	0.003	<1	(1)
Cancer	0			0.005	<1	(1)
Crabs	0			0.002	<1	(1)
Snails	0.002	<1	(1)	0		
Total	10.148	100		6.268	100	

by the 0+ and 1+ age classes observed by Moring (1981) were similar to those displayed by the Dillon Beach age 0+ and 1+ classes; however, Moring observed age 2+ individuals of up to 101 mm SL. Nakamura (1976a, b) also reported collecting *O. snyderi* >80 mm SL at Port Renfrew, British Columbia. These results indicate that *O. snyderi* may have a longer lifespan at more northerly locations. The scarcity of individuals >70 mm SL at Dillon Beach probably did not result from repeated sampling because such large individuals were absent from the initial samples and from collections made in previously unsampled pools near the study site in August 1979, December 1979, and April 1980. There was no discernable pattern in sex-ratio deviations from unity observed in four 1979 collections, which

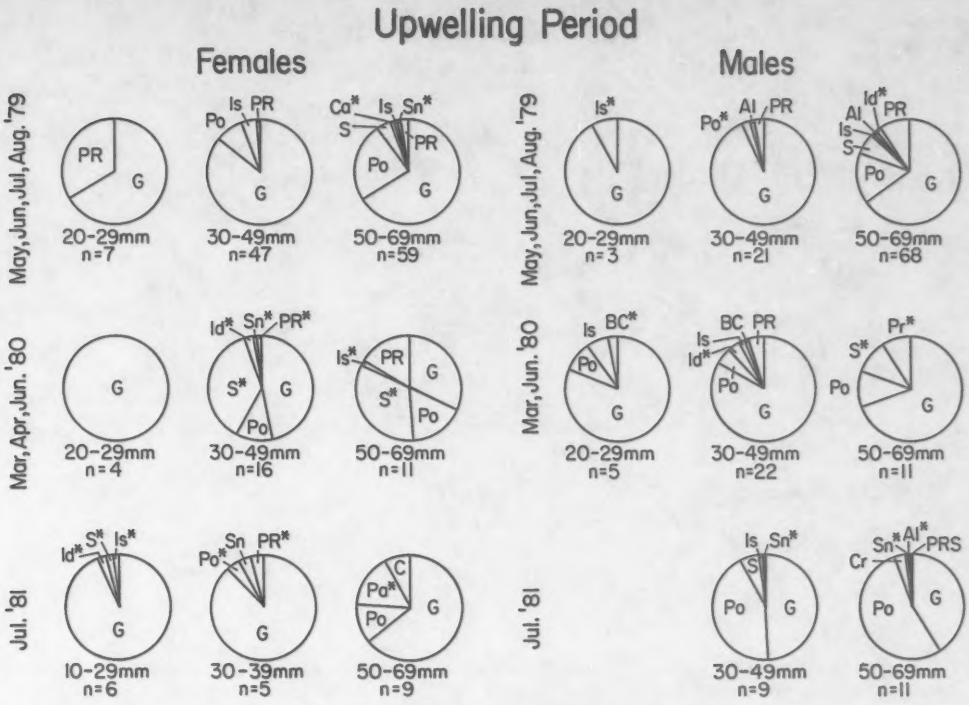

FIGURE 3.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the 1979, 1980, and 1981 Upwelling periods. Prey are represented as percent total prey weight, and only prey composing ≥1% of the total prey weight are shown. Asterisks indicate prey which occurred in only one individual. Prey abbreviations are G (gammarids); PR (hard-bodied prey remains); Po (polychaetes); Is (isopods); S (shrimps, all spp.); Ca (caprellids); Sn (snails); Id (*Idotea* spp.); Pa (*Pagurus* spp.); Cr (crabs, all spp.); Al (algae); and BC (barnacle cirri).

suggests that males and females have about equal lifespans at Dillon Beach.

Oligocottus maculosus Girard, another abundant intertidal cottid (Nakamura 1976a, b; Moring 1981), was estimated by Chadwick (1976) to survive as many as five growing seasons, based on counts of vertebral rings, at Port Renfrew, B.C., and Bruels Point, CA. Annuli were not validated in this study, however, and it is questionable if the rings observed were actually formed once yearly. In addition, Chadwick's (1976) growth rate estimates are extremely low, suggesting that *O. maculosus* grew no more than 7 mm in any season after the first. Moreover, all previous studies of both *O. snyderi* (Moring 1981) and *O. maculosus* (Atkinson 1939; Green 1971; Moring 1979) showed that populations of these species were composed primarily of age 0+ and 1+ individuals, as was *O. snyderi* at Dillon Beach. Consequently, it appears unlikely that *O. maculosus* survives to age 5+ as suggested by Chadwick (1976), and in any case such longevity was not observed for *O. snyderi* at Dillon Beach.

Intertidal fishes appear to display several distinct life history patterns. Short lifespan (1-3 yr), early maturation, and high reproductive effort have been reported for several intertidal gobies in northern temperate habitats (Gibson 1969, 1982; Grossman 1979; Miller 1979). In contrast, lifespans of 4 to over 10 yr, accompanied by delayed maturation, have been observed in many intertidal species, including gobiids and blenniids (Gibson 1969, 1982; Stephens et al. 1970; Grossman 1979; Miller 1979). Little information is available for intertidal cottids. The largest North American cottid, *Scorpaenichthys marmoratus* Ayers, may live 13 yr, but only inhabits tidepools during its first or second year of life (O'Connell 1953; Grossman and Freeman unpubl. data). Another large sculpin, *Leptocottus armatus* Girard, common in the Pacific coast bays and estuaries, is known to live to age 3 and reaches sexual maturity

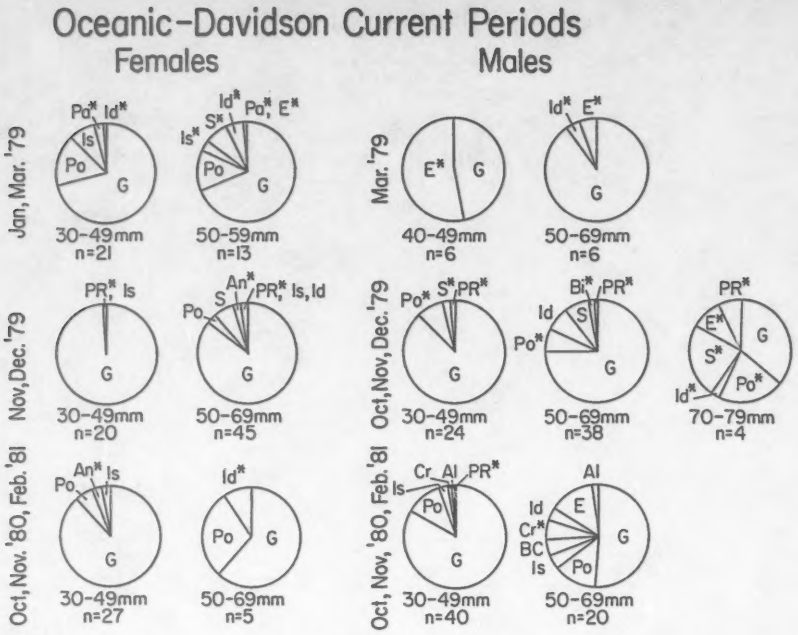

FIGURE 4.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the three ODC (Oceanic-Davidson Current) periods encompassed by this study. Prey are represented as percent total prey weight; only prey composing ≥1% total prey weight are shown. Asterisks indicate prey occurring in only one individual. Abbreviations are as in Figure 3, with the addition of E (eggs); An (sea anemones); and Bi (bivalves).

after 1 yr (Jones 1962; Tasto 1975). *Oligocottus snyderi* and *O. maculosus* apparently are best characterized by the short lifespan, early maturation, life history pattern. This conclusion is based on growth rate data coupled with the scarcity of individuals older than 1.5 yr, and data showing early maturation and high reproductive effort for *O. snyderi* (deVlaming et al. 1982).

The majority of age 0+ *O. snyderi* at Dillon Beach attained sufficient size to spawn during their first year; it is less certain what proportion of these individuals survive to spawn in their second year. Grossman and deVlaming (1984) indicated that, at Dillon Beach, females mature at about 40 mm SL and contain vitellogenic oocytes from October through May. These females also probably spawn more than once, primarily during winter and spring (Grossman and deVlaming 1984). Length-frequency distributions from March and May 1979 and March and April 1980 show that a single age class dominated the population. Hence, assuming that recruitment primarily was derived from this population, age 1+ individuals (recruited the previous spring and summer) must have been responsible for nearly all spring spawning. The paucity of large individuals (i.e., >60 mm SL) in winter or spring samples indicates that if individuals spawned in their second year, this reproduction must have occurred prior to January. Substantial numbers of age 1+ individuals were captured from October to December 1979 and in November 1980. Although the earliest recruitment observed at Dillon Beach occurred in March 1980, Moring (1981) captured newly recruited individuals as early as January. This suggests that fall spawning may occur in more northerly populations of *O. snyderi*.

Reproduction apparently is timed to insure that larvae metamorphose during upwelling. Grossman (1982) found a significant correlation between upwelling activity and the number of resident species with young-of-the-year present at Dillon Beach. Grossman and deVlaming (1984) also observed that *O. snyderi* recruitment was strongly correlated with productivity; the authors pointed out that the early

recruitment observed in March 1980 coincided with the onset of upwelling, whereas both recruitment and upwelling were delayed until May 1979.

If some individuals do survive to reproduce during their second year, the larger sizes attained by males during their second growing season may be advantageous during spawning. This is because male *O. snyderi* have a lengthened and prehensile first anal ray with which they clasp females during copulation, and the larger a male is in relation to a female, the more efficiently he will be able to clasp her (Morris 1956).

Dietary Habits

Oligocottus snyderi at Dillon Beach consumed primarily gammarid amphipods and polychaetes. These data are consistent with previous observations (Johnston 1954; Nakamura 1971; Yoshiyama 1980), although they differ somewhat from results obtained by Cross (1981) from two sites in northern Washington. Cross (1981) reported that harpacticoid copepods were a major prey for *O. snyderi* at one site; similarly, polychaetes also were consumed only at one site. However, Cross (1981) also observed high gammarid consumption by *O. snyderi*, as well as by most other intertidal species he studied. In addition, gammarids have been cited as a major prey in other intertidal fish assemblages (Mitchell 1953; Johnston 1954; Zander 1979, 1982; Grossman in press b). At Dillon Beach, gammarids frequently were consumed by resident and seasonal intertidal fishes, although only one other resident (*Apodichthys flavidus* Girard) possessed a diet dominated by gammarids (Grossman in press b). Among year, seasonal comparisons, however, show that a variety of minor prey types also are consumed by *O. snyderi*.

Combinations of shrimps, crabs, hermit crabs, *Idotea*, and other irregularly consumed prey constituted a considerable proportion of *O. snyderi*'s diet throughout the year. This was particularly evident in larger fish, which suggests that capture of these prey is either more difficult for small fish due to morphological, physiological, or behavioral constraints, or involves increased predation risk. Similarly, a shift from gammarids to larger prey concomitant with increasing length was observed for the majority of intertidal fishes at Dillon Beach (Grossman in press b), and for some species studied by Cross (1981). In contrast, Yoshiyama (1980) was unable to detect dietary differences between small and large *O. snyderi*, or two other intertidal cottids. Yoshiyama pooled small samples collected throughout a year, however, which may have obscured seasonal changes in prey consumption. Because his samples were small, Yoshiyama also may have underestimated consumption of rare prey.

Although seasonal dietary changes were minor, there is evidence that females possessed higher ingestion rates than males during the ODC period. During this season of lowered productivity, females consumed two times more gammarids (by weight) than males, although mean fish length and gammarid frequency of occurrence were nearly identical between sexes. This difference between consumption rates may not be artifactual. Females develop and carry vitellogenic eggs during this period (Grossman and deVlaming 1984), and consequently have high energy demands. There was no evidence that intersexual or ontogenetic dietary differences resulted from differential distribution or collection disturbance.

The high prey weight observed in males and females collected during the ODC period is of interest in light of the low growth rates observed during winter months. Moring (1979, 1981) also observed cessation of growth during winter for both *O. snyderi* and *O. maculosus* in northern California. He suggested that reduced foraging activity caused by increased wave action during winter might partially explain this growth reduction. Dietary data from Dillon Beach do not support this conclusion because ODC specimens contained a greater total weight of prey than individuals collected during Upwelling, even though a greater number of individuals were examined during the latter period. The Dillon Beach study site probably is more sheltered from winter storm activity, however, than the Trinidad Bay sites observed by Moring (Grossman pers. obs.). In the absence of ingestion rate data for both seaons, results based on gut content weight alone are equivocal. Moring (1981) also suggested that gonadal development during the winter months might be responsible for reduced growth; this could also apply to *O. snyderi* at Dillon Beach.

In conclusion, *O. snyderi* the most abundant intertidal cottid at Dillon Beach, possesses a suite of characteristics which suggest that productivity has influenced the biology and behavior of this species. For example, *O. snyderi* reaches sexual maturity during its first year of life, and spawns at a time which enables recruitment to take place during the season of highest productivity (i.e., Upwelling (Grossman and deVlaming 1984)). Grossman (1982, in press b) presented strong evidence that productivity cycles also affect many other species at Dillon Beach, because this assemblage appears to be organized through interspecific exploitative competition for

food. Recuitment and numerical abundances within this assemblage also were strongly correlated with productivity (Grossman 1982). *Oligocottus snyderi* possesses a variety of adaptations (e.g., rapid maturation, high female reproductive effort, utilization of an abundant prey not widely consumed by other assemblage members) which probably are responsible for its numerical dominance in a fluctuating environment.

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LITERATURE CITED

ATKINSON, C. E.
1939. Notes on the life history of the tidepool johnny (*Oligocottus maculosus*). Copeia 1939:23-30.

BOLIN, R. L., AND D. P. ABBOTT.
1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23-45.

CHADWICK, E. M. P.
1976. A comparison of growth and abundance for tidal pool fishes in California and British Columbia. J. Fish Biol. 8:27-34.

CROSS, J. N.
1981. Structure of rocky intertidal fish assemblage. Ph.D. Thesis, Univ. Washington, Seattle, 259 p.

DEVLAMING, V., G. D. GROSSMAN, AND F. CHAPMAN.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.

GARRISON, D. L.
1979. Monterey Bay phytoplankton. I. Seasonal cycles of phytoplankton assemblages. J. Plankton Res. 1:241-265.

GIBSON, R. N.
1969. The biology and behavior of littoral fish. Oceanogr. Mar. Biol. Annu. Rev. 7:367-410.
1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Annu. Rev. 20:363-414.

GREEN, J. M.
1971. Local distribution of *Oligocottus maculosus* Girard and other tidepool cottids of the west coast of Vancouver Island, British Columbia. Can. J. Zool. 49:1111-1128.

GROSSMAN, G. D.
1979. Demographic characteristics of an intertidal bay goby (*Lepidogobius lepidus*). Environ. Biol. Fishes 4:207-218.
1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119:611-637.
In press a. Long term persistence in a rocky intertidal fish assemblage. Environ. Biol. Fishes.
In press b. Division of food resources among fish of the rocky intertidal zone. J. Zool. (Lond.).

GROSSMAN, G. D., AND V. DEVLAMING.
1984. Reproductive ecology of female *Oligocottus snyderi* Greeley: a North American intertidal sculpin. J. Fish Biol. 25:231-240.

JOHNSTON, R. F.
1954. The summer food of some intertidal fishes of Monterey County, California. Calif. Fish Game 40:65-68.

JONES, A. C.
1962. The biology of the euryhaline fish *Leptocottus armatus armatus* Girard (Cottidae). Univ. Calif., Publ. Zool. 67: 321-367.

LEVINS, R.
1968. Evolution in changing environments. Princeton Univ. Press, Princeton, 120 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish. Bull. 157, 235 p.

MILLER, P. J.
1979. Adaptiveness and implications of small size in teleosts. *In* P. J. Miller (editor), Fish phenology: anabolic adaptiveness in teleosts, p. 263-306. Zool. Soc. Lond. Symp. 44.

MITCHELL, D. F.
1953. An analysis of stomach contents of California tidepool fishes. Am. Midl. Nat. 49:862-871.

MORING, J. R.
1979. Age structure of a tidepool sculpin, *Oligocottus maculosus*, population in northern California. Calif. Fish Game 65:111-113.
1981. Seasonal changes in a population of the fluffy sculpin, *Oligocottus snyderi*, from Trinidad Bay, California. Calif. Fish Game 67:250-253.

MORRIS, R. W.
1956. Clasping mechnisms of the cottid fish *Oligocottus snyderi* Greeley. Pac. Sci. 10:314-317.

NAKAMURA, R.
1971. Food of two cohabiting tide-pool Cottidae. J. Fish. Res. Board Can. 28:928-932.
1976a. Experimental assessment of factors influencing microhabitat selection by two tidepool fishes *Oligocottus maculosus* and *O. snyderi*. Mar. Biol. (Berl.) 37:97-104.
1976b. Temperature and the vertical distribution of two tidepool fishes (*Oligocottus maculosus, O. snyderi*). Copeia 1976: 143-152.

O'CONNELL, C. P.
1953. Life history of the cabezon *Scorpaenichthys marmoratus* (Ayres). Calif. Dep. Fish Game, Fish. Bull. 93, 76 p.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

STEPHENS, J. S., JR., R. K. JOHNSON, G. S. KEY, AND J. E. MCCOSKER.
1970. The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). Ecol. Monogr. 40:213-233.

TASTO, R. N.
1976. Aspects of the biology of the Pacific staghorn sculpin, *Leptocottus armatus* Girard, in Anaheim Bay. Calif. Dep. Fish Game, Fish. Bull. 165:123-135.

YOSHIYAMA, R. M.
1980. Food habits of three species of rocky intertidal sculpins (Cottidae) in central California. Copeia 1980:515-525.

1981. Distribution and abundance patterns of rocky intertidal fishes in central California. Environ. Biol. Fishes 6:315-332.

ZANDER, C. D.

1979. On the biology and food of small-sized fish from the North and Baltic Sea areas. II. Investigations of a shallow stony ground off Møn, Denmark. Ophelia 18:179-190.

1982. Feeding ecology of littoral gobiid and blennioid fish of the Banyuls area (Mediterranean Sea). I. Main food and trophic dimension of niche and ecotope. Vie Milieu 32:1-10.

VARIABILITY, TRENDS, AND BIASES IN REPRODUCTIVE RATES OF SPOTTED DOLPHINS, *STENELLA ATTENUATA*

JAY BARLOW[1]

ABSTRACT

Temporal changes were examined in three parameters that affect reproduction of spotted dolphin populations in the eastern Pacific. Of mature females, percent pregnant decreased markedly from the period 1971-73 to the period 1974-83. Within the period 1974-83, percent pregnant remained relatively constant. Of pregnant females, percent lactating increased during the period 1971-83. The percentage of sexually mature females did not change. Potential biases in the measurement of the three parameters were identified by examining the effects of sampling conditions. The percentage of mature females that are pregnant and the percentage of pregnant females that are lactating were found to be robust to sampling conditions. The percentage of mature females in a sample was found to depend significantly on the number of dolphins killed per set, and annual variability was too large to be explained by random sampling error. Comparisons between two populations show that the more exploited population has a lower percent pregnant, although the opposite might be expected from density compensatory effects. Percent lactating and percent immature were higher in the more exploited population.

Changes in the reproductive parameters of cetacean populations can be used to make inferences about the status or general "health" of a population. For instance, increases in pregnancy rates and decreases in the age at attainment of sexual maturity were linked to reductions in Antarctic whale populations (Gambell 1975). Re-analysis of these data, however, revealed unsuspected biases, and Gambell's results are now being questioned (Mizroch 1983). The purpose of this paper is to examine potential biases in measuring reproductive rates of spotted dolphins, *Stenella attenuata*. This species is taken incidentally in the tuna purse seine fishery in the eastern tropical Pacific (Smith 1983). The intent is to determine whether reproductive rates can be measured with sufficient precision to monitor intrapopulation changes or to make interpopulation comparisons.

Previous studies of female reproduction in spotted dolphins of the eastern Pacific have shown an apparent decrease in pregnancy rates from 1973 to 1975 (Perrin et al. 1977), from 1973 to 1978,[2] and from 1971 to 1978 (Hester 1984). Hester (1984) suggested that this decline in pregnancy rates is related to the decline in fishing-related dolphin mortality during the same time period.

Three indices of the reproductive status of female spotted dolphins are examined in the present paper: 1) the fraction of sexually mature individuals that are pregnant, 2) the fraction of pregnant females that are lactating, and 3) the fraction of females that are sexually mature. These measures have been used previously in calculating what has been termed the gross annual reproductive rate (GARR) of spotted dolphins (Perrin et al. 1976). This paper reexamines data from 1971 to 1978 plus additional data from 1979 to 1983 to determine whether the previously noted trends in reproductive rates are real, and if so, whether they are continuing. Also, factors are examined which may be biasing estimates of reproductive rates and which could be causing spurious changes in apparent pregnancy rates and GARR. Finally, differences in these reproductive indices between two geographic stocks of spotted dolphin are discussed in view of their different histories of incidental fishing mortality.

MATERIALS

Reproductive data were collected from a sample of the dolphins killed in tuna purse-seining operations in the eastern tropical Pacific (ETP). Three stocks of spotted dolphins are recognized in this area based on morphological differences (Perrin et al. 1979). Samples considered here include two of these: the northern offshore stock which has been subject to tuna fishing since 1959 and the southern offshore stock which has been subject to exploitation since

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[2]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Admin. Rep. LJ-80-02, 51 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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the early 1970's. In 1971 and 1972, field technicians collected samples predominantly from females with the "adult" or fused color pattern (Perrin 1970). Beginning in 1973, field technicians were instructed to collect samples nonselectively with respect to size and sex. Operationally, this meant working-up specimens in the order in which they appeared on the deck of the tuna vessel. Sampling methods and laboratory procedures are described in detail by Perrin et al. (1976). Sample locations are shown in Figure 1.

Reproductive tracts of mature and nearly mature females were preserved in the field for laboratory examination. In 1971 and 1972, the definition of "mature and nearly mature" was not explicit. In 1973, "mature and nearly mature" was defined as individuals with "mottled" or "fused" developmental color phases (Perrin 1970). Because females in the younger "speckled" color phase occasionally were found to be pregnant, "mature and nearly mature" was redefined operationally (beginning in 1974) as specimens >150 cm total length (TL, measured from tip of rostrum to fluke notch). Laboratory examination of preserved ovaries was used to determine the presence of corpora from past ovulations. Pregnancy was determined by visual examination of the uterus (in later years, fetuses >30 cm TL were removed and measured in the field). Mammary glands were slit and checked in the field for the presence of milk.

In addition to the above life history information, field technicians collected data pertaining to conditions under which the samples were taken. Information used in this report includes the observer's estimate of the size of the school from which the sample was taken, the duration of the chase before the net was set, the number of dolphins known to be killed during fishing operations, and the geographic location at which the sample was taken.

METHODS

Three indices of female reproduction are considered in this paper: the percent pregnant, the percent lactating, and the percent mature. Temporal trends in these three indices were examined by regressing annual means against year (weighting by the inverse of binomial variances).

In calculating the percentages of mature females that were pregnant and that were lactating, specimens were used only if both ovaries were collected and if at least one corpus of ovulation (corpus albicans or corpus luteum) was present. Previously, 1971 and 1972 samples were excluded from calculation of percent pregnant because of undersampling of younger females with a mottled color pattern (Perrin et al. 1977). This was not deemed necessary in this study, because in 1973-83 samples the percent pregnant for mature mottled females (31.1%) was essentially the same as that for mature females with a fused color pattern (31.4%).

In calculating the percentage of females that were sexually mature, two different criteria were used for determining maturity. In the majority of cases both ovaries were examined, and the presence of one (or more) corpus of ovulation was taken as evidence of sexual maturity. If ovaries were not collected or examined (which was true for about 30% of females over 150 cm TL), a length criterion was used for maturity. Samples from 1971 and 1972 were excluded from these analyses because sampling was not random in those years.

"Length at attainment of sexual maturity" was determined by the method used by Perrin et al. (1977). Based on the sample for which ovaries were examined, this length was estimated as the length at which the number of longer immature individuals equals the number of shorter mature individuals. For the northern stock, the length at the onset of sexual maturity was determined independently for each year 1974-83 (176.5, 177.5, 177.0, 177.0, 178.0, 177.5, 179.0, 178.5, 180.0, and 182.0 cm, respectively). In 1973 the decision to collect ovaries was not based on specimen length. The apparent trend in these data yields a significant regression (P = 0.0008); hence, regression estimates were substituted for annual estimates for 1974-83, with an extrapolation to 1973. These values were 175.6, 176.1, 176.6, 177.1, 177.6, 178.0, 178.5, 179.0, 179.5, 180.0, and 180.5 cm, respectively, for 1973-83. For the southern stock, insufficient data exist to calculate a length at attainment of sexual maturity for individual years, hence the collective value was used for all years (175.0 cm).

Six factors were examined to determine whether annual changes in the above percentages of pregnant females were caused or affected by changing biases in the sampling methods. These factors include 1) geographical provenance, based on two strata (Fig. 1) which roughly correspond to the historical tuna fishing grounds (inside the Commission Yellowfin Regulatory Area, CYRA) and a more recently exploited area (outside the CYRA); 2) the quarter of the year; 3) the length of chase, or the time between sighting the dolphin school and capture (net set); 4) the observer's estimate of the dolphin school size (only available since 1973); 5) the number of dolphins known to have been killed in the set; and 6) the total number of tons of tuna caught in the set.

The selection of these six factors was guided to

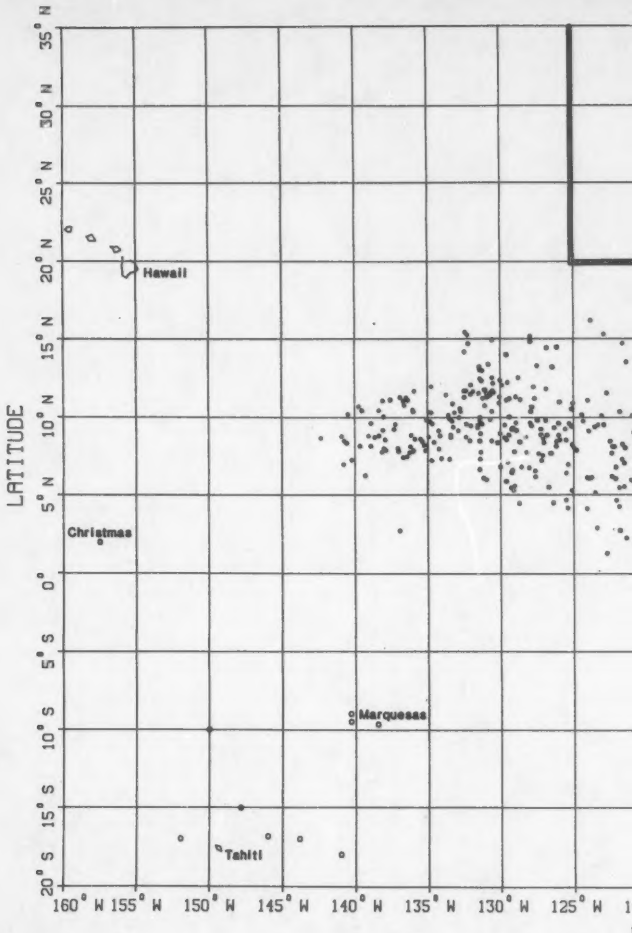
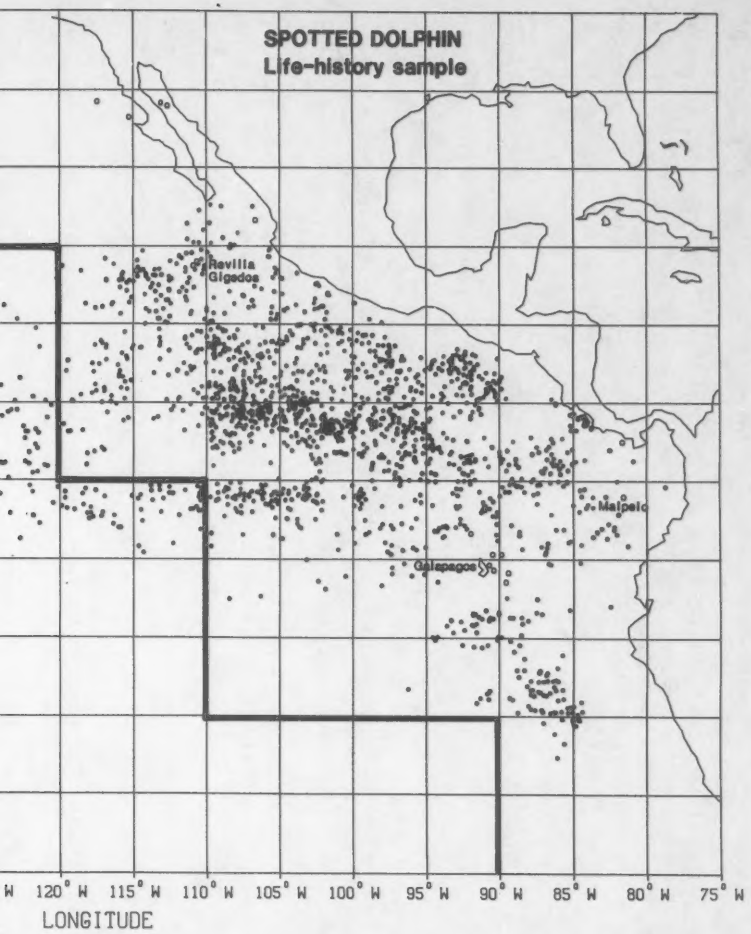


FIGURE 1.—Locations at which male and female spotted dolphins were collected for life hist
studies, 1968-83. Bold line indicates western border of the Commission Yellowfin Regulat
Area (CYRA). Figure taken from Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. C


SPOTTED DOLPHIN
Life-history sample
Revilla Gigedos
Malpelo
Galapagos
W 120° W 115° W 110° W 105° W 100° W 95° W 90° W 85° W 80° W 75° W
LONGITUDE

fe history
egulatory
. L. Cass.

1984. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Admin. Rep. LJ-84-02, available from NOAA, Southwest Fisheries Center, La Jolla, CA 92038.

some extent by previous studies. The sex ratio and the fraction of yearling dolphins in a sample were found to vary with kill size (No. 5 above). The fraction of neonatal animals in tuna-vessel samples was found to vary significantly with area, season, chase time, dolphin kill, and tuna catch (Nos. 1, 2, 3, 5, and 6 above)[3]. Preliminary work by A. A. Hohn[4] and M. D. Scott[5] has indicated that immature spotted dolphins may segregate into schools with different characteristic school sizes (No. 4 above).

The significance of each of the above factors was tested separately using a Pearson chi-square. For each test, the null hypothesis was that either percent pregnant, percent lactating, or percent mature is independent of the factor being tested. If this hypothesis is shown to be false, then it is likely that reproductive parameters may be affected by sampling bias. Unfortunately, the above sampling factors are not independent; a factor may appear significant when, in fact, that factor is merely correlated with a causative factor. Because of this, probablilties should be interpreted with caution.

Multiway comparisons were used to discriminate factors which are truly important from those which are correlated to significant factors. A hierarchical approach was used, based on the log-linear model for discrete multivariate analysis (program BMDP4F, Dixon 1981). The above 2-way tests were used to identify factors that may be significant. The factors that were significant in the 2-way tests were used in 3-way tests. The factors which proved significant in the 3-way tests were then included in 4-way tests (which proved to be a practical upper limit on multiway tests using our data set). In this manner, multiway comparisons of factors could be tested, whereas a 7-way test of all factors would not have been feasible.

Analysis of variance (ANOVA) was tried and rejected as an alternative to the log-linear model for multiway comparisons. The method used in this trial was to calculate percent pregnant for each set and to use sets as replicates in an ANOVA. Although ANOVA is recognized to be robust to violations in assumptions, the sample size for individual sets is very small (mean number of mature females per set is 1.6, mode is 1). As a result, the percent pregnant in 72% of sets was either 0% or 100% of mature females. No transformation was able to normalize these data. Using an arc-sine transformation, 2-way ANOVA was not even able to recognize the four significant factors affecting percent pregnant that were identified using a simple Pearson chi-square. Because of these problems, the ANOVA model was rejected for use in the multiway comparisons.

RESULTS

Percent Pregnant

The fractions of sexually mature females that were pregnant are given in Table 1 for the samples of the northern and southern offshore stocks collected from 1971 to 1983. Sample sizes decline in the later years for the northern stock, but are typically >100.

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, 7 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[4]A. A. Hohn, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

[5]M. D. Scott, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

TABLE 1.—Fractions a) of females that were sexually mature, b) of sexually mature females that were pregnant, and c) of pregnant females that were lactating. Samples include 1971-83 specimens from the northern and southern offshore stocks of spotted dolphins. Fraction mature was not sampled in 1971 and 1972.

	Year													
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Overall
Northern stock														
a) Fraction mature			0.56	0.53	0.54	0.50	0.61	0.59	0.59	0.55	0.61	0.56	0.50	0.561
Number in sample			1,149	1,013	1,215	751	995	564	593	509	465	579	137	7,970
b) Fraction pregnant	0.48	0.41	0.42	0.29	0.29	0.34	0.27	0.24	0.30	0.30	0.29	0.32	0.38	0.329
Number mature	79	449	573	487	493	291	375	229	205	148	153	148	37	3,667
c) Fraction lactating	0.26	0.08	0.08	0.17	0.14	0.13	0.35	0.15	0.30	0.23	0.24	0.19	0.28	0.162
Number pregnant	38	180	236	138	130	93	94	52	61	43	42	47	14	1,168
Southern stock														
a) Fraction mature			0.58	—	0.68	0.63	0.61	0.77	0.58	0.73	0.60	0.70	0.69	0.656
Number in sample			24	0	38	254	23	51	166	59	20	199	106	940
b) Fraction pregnant	—	—	0.75	—	0.49	0.48	0.12	0.28	0.22	0.35	0.00	0.32	0.18	0.364
Number mature	0	0	12	0	23	145	8	25	60	17	8	73	22	393
c) Fraction lactating	—	—	0.00	—	0.22	0.04	0.00	0.16	0.08	0.00	—	0.23	0.00	0.087
Number pregnant	0	0	9	0	9	68	1	6	13	6	0	22	4	138

Samples sizes for the southern stock are highly variable between years, and several years have too few specimens to reliably estimate the fraction of the population that would be pregnant. For 1973-83, the overall percentage of pregnant females is, however, significantly higher for the southern stock, 36.4%, than for the northern stock, 31.4% (χ^2_1 = 3.97, P = 0.05). Because of this difference, northern and southern stocks were not pooled in subsequent analyses. Due to the small sample size from the southern stock, examination of trends and biases in female reproductive rates was limited to the northern stock.

Annual estimates of the percentage of pregnant females are illustrated in Figure 2 for the northern offshore stock. The regression is significant; however, the residuals do not appear randomly distributed. The negative slopes of the regression lines are largely due to high pregnancy rates in 1971-73. Expected values for the percent pregnant in each year were generated in two ways: from the overall percent pregnant and from the "de-trended" regression predictions. Chi-square tests using these expected values show the annual variability in percent pregnant is greater than would be expected from random sampling of a population with a constant ($P < 0.001$) or linearly decreasing ($P < 0.001$) pregnancy rate.

Although natural year-to-year variability in pregnancy rates cannot be ruled out, a changing bias in sampling could also cause larger than expected variability in percent pregnant. To look for such a bias, the sample from the northern stock was stratified by the six sampling factors described above. The percent pregnant in each of these strata is given in Table 2, with the chi-square probabilities that the samples could have been drawn randomly from the pooled sample. Of the factors examined, pregnancy rate was significantly related to sampling season, dolphin kill-per-set, and tuna catch-per-set (henceforth the latter two are referred to as kill and catch).

Because sampling seasons, mean dolphin kills, and mean tuna catches vary significantly between years, these factors cannot be considered independent of year. For instance, the interaction between pregnancy rates and dolphin kill might appear significant due to high kill rates or high catch rates in a year (or years) that coincidentally had high pregnancy rates. Conversely, high pregnancy rates in one year may be due to a sampling bias related to dolphin kill.

Multiway tests were used to identify possible interactions between the three significant factors and year effects. In all cases, 3-way tests indicate that year effects are significant (Table 3). First order effects of kill, catch, and season were not significant; however, higher order effects involving the latter two were important (Table 3). A 4-way test using catch, season, and year also shows significant higher order interactions involving both catch and season (Table 3).

Higher order interactions involving year and another factor indicate that effect of that factor changes with year. Since pregnancy rates appear to have changed markedly from 1971-73 to 1974-83 (Fig. 2), the effect of the significant factors was

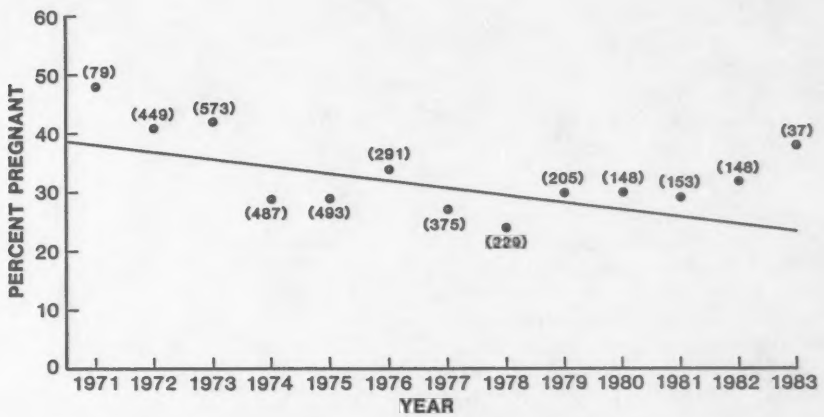


FIGURE 2.—Percentages of mature females that were pregnant for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid line represents weighted regression. Sample sizes are in parentheses.

TABLE 2.—Percentage of sexually mature females that were pregnant (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Pregnant (%)	*N*	Probability
1) Geographic area			
Inside CYRA	33.5	3,032	0.09
Outside CYRA	30.0	633	
2) Season			
1st quarter	34.7	1,799	
2d quarter	33.5	741	0.04
3d quarter	28.9	584	
4th quarter	30.4	542	
3) Chase time (min)			
<20	31.2	1,081	
20-40	34.8	1,440	0.09
>40	31.1	747	
4) School size			
<500	30.2	443	
500-1,500	29.8	741	0.49
>1,500	27.4	693	
5) Number killed			
1-10	29.8	1,104	
11-30	30.1	917	<0.001
>30	37.4	1,301	
6) Tuna caught (tons)			
0-5	29.0	428	
6-15	33.0	848	0.02
16-30	30.4	760	
>30	35.6	1,280	

tested separately for these two time periods. When the years 1971-73 were excluded (Table 4), the interactions between percent pregnant and season, dolphin kill, and tuna catch are no longer significant. When tests are performed on data from 1971 to 1973 alone (Table 4), season and tuna catch are still significantly related to pregnancy rate.

Percent Lactating

Annual trends in percent lactating for the northern stock of spotted dolphins are illustrated in Figure 3. Two cases are considered: 1) the percentage of all mature females that are lactating and 2) the percentage of pregnant females that are lactating. For both cases, a weighted regression shows a significant increase in the fraction of lactating females through time ($P < 0.05$). In the former case, the regression again appears to be driven by anomalous values in 1971-73. Percentages and sample sizes for the latter case are presented in Table

TABLE 3.—Multiway tests of factors affecting percent pregnant. Log-likelihood chi-square was used to calculate the probability that percent pregnant is independent of the stated factor(s) using the log-linear model. Pregnancy state (pregnant/not pregnant) is implicit as the first factor in each comparison.

Tests	Probability
3-way	
a) Year	<0.0001
Season	0.70
Year × season	<0.0001
b) Year	<0.0001
Kill	0.09
Year × kill	0.31
c) Year	<0.0001
Catch	0.14
Year × catch	0.0004
4-way	
Year	<0.0001
Season	0.90
Catch	0.15
Year × season	<0.0001
Year × catch	0.0002
Season × catch	0.003
Year × season × catch	0.07

TABLE 4.—Percentage of sexually mature females that were pregnant, grouped by season, dolphin kill, and tuna catch. The years 1971-73 and 1974-83 are grouped separately. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included.

Year	Pregnant (%)	*N*	Probability
1971-73 overall	41.9	1,101	
Season			
1st quarter	44.0	722	
2d quarter	47.6	210	<0.001
3d quarter	—	0	
4th quarter	25.4	169	
Number killed			
1-10	38.0	171	
11-30	39.5	248	0.23
>30	44.1	651	
Tuna caught (tons)			
0-5	37.6	101	
6-15	44.5	247	0.04
16-30	35.0	226	
>30	45.5	490	
1974-82 overall	29.0	2,566	
Season			
1st quarter	28.4	1,077	
2d quarter	27.9	531	0.39
3d quarter	28.9	584	
4th quarter	32.7	373	
Number killed			
1-10	28.3	933	
11-30	26.6	669	0.27
>30	30.6	650	
Tuna caught (tons)			
0-5	26.3	327	
6-15	28.3	601	0.76
16-30	28.5	534	
>30	29.5	790	

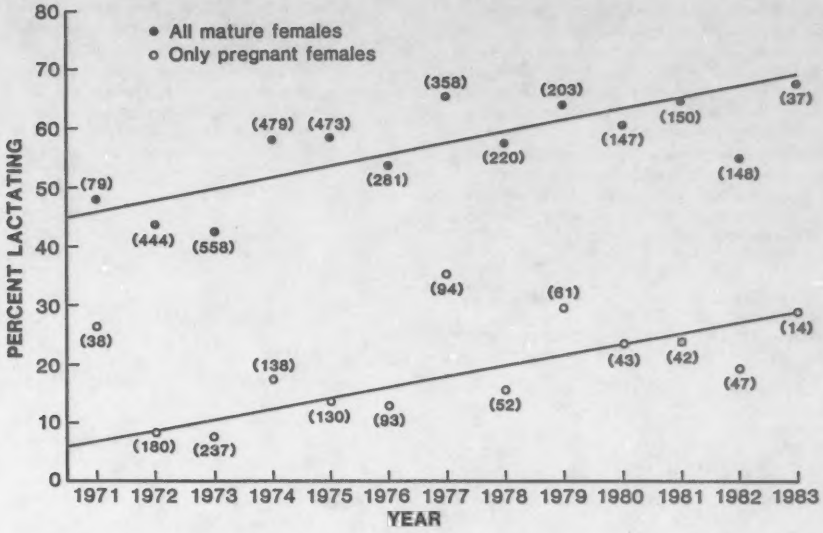


FIGURE 3.—Percentages of mature females that were lactating and percentages of pregnant females that were lactating for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid lines represents weighted regressions. Sample sizes are in parentheses.

1 for both the northern and southern stocks. Again sample size for the southern stock is too small to examine individual years; however, the overall percent of pregnant females that were lactating in 1973-83 samples shows significant differences between stocks ($\chi^2_1 = 6.50$, $P = 0.01$). Annual variability for the northern stock is greater than expected from random sampling of a population with a constant percent lactating ($\chi^2_{12} = 63.5$, $P < 0.001$).

When the sample of pregnant females from the northern stock is stratified by the six sampling factors, lactation state was significantly related to sampling season, dolphin kill, and tuna catch (Table 5). Again, 3-way tests showed that the first order effect of these factors was not significant when year was included as the third factor (Table 6). In each of these cases, the first order effect of year was important. In one case, dolphin kill, a second order interaction between kill and year was also significant.

Percent Mature

The fractions of females that were sexually mature are given in Table 1 by stock and by year (1973-83). Again the sample sizes are sufficient in all years for the northern stock but are inadequate in some years for the southern stock. The southern stock is significantly different from the northern stock in percent mature ($\chi^2_1 = 31.2$, $P < 0.001$), and (given its small sample size) the southern stock was excluded in subsequent stratifications.

The percentage of all females that are mature from 1973 to 1983 is illustrated in Figure 4 for the northern stock. In this case, the weighted regression is not significant. Using chi-square tests, the level of annual variability in percent mature is larger than would be expected from randomly sampling a population with a constant fraction of mature females ($P < 0.001$).

For long-lived animals such as dolphins, annual variability in percent mature should be small and changes in this population parameter should be gradual. Since the annual variability observed in the data is larger than would be expected from random sampling error, year-to-year changes in sampling biases are likely. Percent mature was found to be significantly related to three of the six sampling factors examined: sampling season, dolphin kill-per-set, and tuna catch-per-set (Table 7).

Each of these three significant factors was tested with maturity state and year using 3-way tests (Table 8). For each of these factors, year was a significant factor and all other first order effects were not significant. Only dolphin kill showed a significant second order interaction with year.

TABLE 5.—Percentage of pregnant dolphins that were lactating (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Lactating (%)	*N*	Probability
1) Geographic area			
Inside CYRA	15.7	988	0.30
Outside CYRA	18.8	181	
2) Season			
1st quarter	11.9	611	
2d quarter	17.2	239	<0.001
3d quarter	26.7	161	
4th quarter	20.3	158	
3) Chase time (min)			
<20	14.8	331	
20-40	14.0	479	0.27
>40	18.6	226	
4) School size			
<500	20.0	130	
500-1,000	18.0	211	0.87
>1,500	19.7	183	
5) Number killed			
1-10	19.1	319	
11-30	16.5	267	0.03
>30	12.3	471	
6) Tuna caught (tons)			
0-5	20.5	117	
6-15	16.4	275	0.17
16-30	16.7	221	
>30	12.8	444	

TABLE 6.—Multiway tests of factors affecting the percentage of pregnant females that are lactating. Log-likelihood chi-square was used to calculate the probability that percent lactating is independent of the stated factor(s) using the log-linear model. Lactation state (lactating/not lactating) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	<0.0001
Season	0.29
Year × season	0.007
b) Year	<0.0001
Kill	0.79
Year × kill	0.51

TABLE 7.—Percentage of female dolphins that were sexually mature (1973-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Mature (%)	*N*	Probability
1) Geographic area			
Inside CYRA	55.7	6,329	0.19
Outside CYRA	57.5	1,625	
2) Season			
1st quarter	54.2	3,495	
2d quarter	57.2	1,738	0.02
3d quarter	58.2	1,580	
4th quarter	57.6	1,155	
3) Chase time (min)			
<20	54.4	2,067	
20-40	56.1	3,084	0.36
>40	56.5	1,689	
4) School size			
<500	53.5	1,183	
500-1,500	56.8	1,970	0.19
>1,500	56.0	1,753	
5) Number killed			
1-10	57.9	2,465	
11-30	54.9	2,068	0.02
>30	54.0	2,321	
6) Tuna caught (tons)			
0-5	53.3	920	
6-15	55.1	1,779	0.05
16-30	54.5	1,668	
>30	57.7	2,482	

DISCUSSION

Changes in the reproductive status of the female segment of a population can be monitored using a variety of reproductive indices: 1) mean age at sexual maturation, 2) mean length (or weight) at sexual maturation, 3) annual pregnancy rates, 4) calving interval, 5) percentage of mature females that are pregnant, 6) percentage of females that are lactating, and 7) percentage of females that are sexually mature. Changes in each of these are examined below.

Changes in Maturation Parameters

Myrick et al. (1984) have found no significant difference in the age at sexual maturation (ASM) between a sample from 1973 to 1978 and another sample from 1981. In the present study, length at attainment of sexual maturity is estimated to have increased 4.4 cm from 1974 to 1983. If these results hold, dolphins must be growing faster in recent years. Given small sample sizes of aged individuals, significant changes in ASM may be difficult to detect. Previous studies have shown that the age at sexual maturation is quite responsive to population changes in marine mammals (Fowler 1984), while length at maturation tends to show little change. For fin whales, *Balaenoptera physalus*, Lockyer (1972)

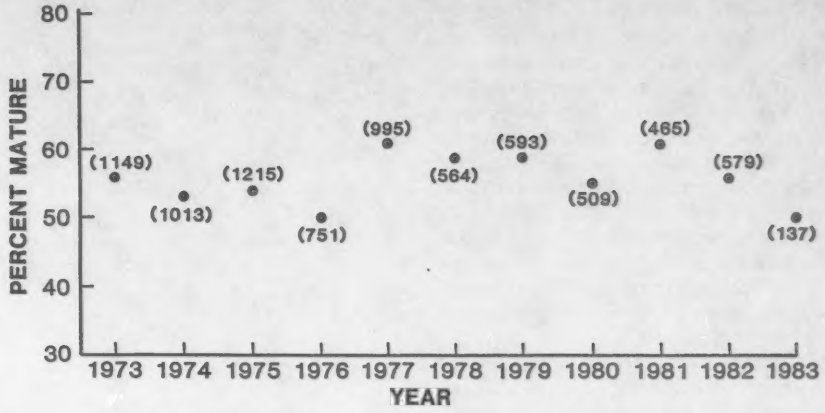


FIGURE 4.—Percentages of all females that were mature for the northern offshore stock of spotted dolphins from 1971 to 1983. Sample sizes are in parentheses.

TABLE 8.—Multiway tests of factors affecting percent mature. Log-likelihood chi-square was used to calculate the probability that percent mature is independent of the stated factor(s) using the log-linear model. Maturation state (mature/not mature) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	0.003
Season	0.49
Year × season	0.08
b) Year	0.003
Kill	0.16
Year × kill	0.002
c) Year	0.0009
Catch	0.09
Year × catch	0.42

showed a decrease in ASM without any change in the length at which maturity is attained. Laws (1956) predicted an inverse relationship between ASM and early growth rates for marine mammals. Spotted dolphins appear to show an increase in length at maturation with no change in ASM, and thus do not follow predicted patterns.

Trends in Percent Pregnant

Annual pregnancy rates, calving interval, and percent pregnant all measure essentially the same thing. Annual pregnancy rate and calving interval require knowledge of gestation times. Because density compensatory responses have not been shown in cetacean gestation times, it is more straightforward to deal directly with percent pregnant.

What appeared to be a rapid decline in dolphin pregnancy rates from 1973 to 1978 (Henderson et al. fn. 2), now appears as two eras with distinctly different pregnancy rates. The fraction of pregnant females in the 1971-73 samples was quite high. The 10 years since 1973 show a lower and relatively constant fraction of pregnant females. This difference in results is due largely to use of a larger sample size and a longer time series.

There is no evidence of the sort of slow, long-term trends in pregnancy rates that might be associated with changes in population sizes. The reason for the dramatic change in pregnancy rates between 1973 and 1974 is not known. At least three hypotheses could be used to explain this change: 1) it was the result of a naturally high pregnancy rate in 1971-73; 2) it was the result of heavy fishing-related mortality of nursing calves prior to 1974 that resulted in artificially high pregnancy rates; or 3) it was the result of a bias in the sampling by tuna vessels.

The first hypothesis suggests that changing environmental conditions result in annual changes in pregnancy rates. In the ETP the largest environmental perturbations are associated with "El Niño" events which occur on the time scale of from 5 to 10 yr (Rasmusson and Carpenter 1982). El Niño conditions prevailed in 1972 (moderate), 1975-76 (weak), and 1982-83 (very strong). These dates do not help explain the change in pregnancy rates that occurred between 1973 and 1974.

The second hypothesis is that heavy dolphin mortality in the 1960's and early 1970's may have somehow affected dolphin pregnancy rates. Large reduc-

tions in dolphin mortality occurred following the passage of the Marine Mammal Protection Act of 1972 (Table 9). If mortality rates were higher for nursing calves, calving interval might have been shortened. This would result in higher pregnancy rates and lower lactation rates, both of which were observed in 1971-73. Analyses have indicated that very young calves are more susceptible to tuna-net mortality (Powers and Barlow fn. 3; Stuntz[6]). Indirectly, high calf mortality may also result from the separation of a calf from its mother during long chases. It is not known if the magnitude of these effects could have resulted in the observed changes in pregnancy or lactation rates.

The third hypothesis is that sampling methods were somehow different between 1971-73 and 1974-83. The only difference in the sampling design was that in 1971-73, scientific technicians were placed only on tuna vessels that agreed to cooperate. Beginning in 1974, the selection of vessels was random. It is difficult, however, to see how this change would affect the percent pregnant in the samples. As was noted above, percent pregnant was significantly correlated with sampling season, dolphin kill-per-set, and tuna catch-per-set during the years 1971-73, but not during the years 1974-83. The reason for this difference is not known, but this would seem to be evidence that sampling was more random in the latter period.

The observed change in percent pregnant from 1971-73 to 1974-83 cannot be explained with certainty. The high pregnancy rates in 1971-73 can be logically explained by direct or indirect effects of the fishery or by sampling biases in those years (Hypotheses 2 and 3). Determining whether either (or both) hypothesis is true may not be possible with existing data.

Trends in Percent Lactating

Changes were also found in the percentage of lactating females. For mature females, the fraction lactating shows low values in 1971-73 and high values in 1974-83, which is opposite the pattern seen for fraction pregnant. This inverse correlation would be expected given that pregnancy state and lactation state are physiologically linked (i.e., cessation of lactation leads to ovulation and pregnancy). Perhaps more meaningful is the increase in the fraction of pregnant females that were lactating. Because being simultaneously pregnant and lactating represent the greatest energy drain on female dolphins, this quantity is likely to be very sensitive to changes in environmental conditions. Because nonpregnant females are excluded, this quantity should also be insensitive to sample biases that are related solely to pregnancy state.

Given that no trends were seen in the percent pregnant from 1974 to 1983, we can infer that the calving interval, or the mean period between births for a mature female, also did not change during that time. If calving interval were constant, the increase in the fraction of pregnant females that were lactating indicates that females may be nursing their calves for a longer period of time, hence a longer lactation period. This increase in the lactation period may have resulted from a decrease in fishery related calf mortality during the 1971-83 period. Because calves may be more susceptible to death or separation from their mothers during the chase, capture, and release of a dolphin school, mean lactation periods may have been abbreviated during the earlier years (Hypothesis 2 above).

TABLE 9.—Estimates of numbers of spotted dolphins killed by all purse seine vessels in the eastern tropical Pacific, 1968-78 (data from Smith 1983).

Year	Spotted dolphins killed
1968	178,000
1969	365,000
1970	355,000
1971	176,000
1972	288,000
1973	131,000
1974	95,000
1975	105,000
1976	47,000
1977	22,000
1978	19,000

Trends in Percent Mature

No significant trends in the percentage of females that were sexually mature during 1971-83 are evident for the northern stock of spotted dolphins. Annual variability was far too great to be explained by random sampling error. This parameter showed a significant correlation with dolphin kill-per-set. Therefore, unless sampling conditions remain constant (which they have not), percent mature is not a useful index for monitoring reproductive capability of the spotted dolphin populations.

[6]Stuntz, W. E. 1980. Variation in age structure of the incidental kill of spotted dolphins, *Stenella attenuata*, in the U.S. tropical purse-seine fishery. Admin. Rep. LJ-80-06, 29 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Variability in percent mature with sampling conditions may result from several interacting factors. Preliminary data have indicated that spotted dolphins in the ETP may segregate on the basis of reproductive maturity (A. A. Hohn fn. 4 and M. D. Scott fn. 5). Schools that consist principally of immature dolphins may have a smaller characteristic school size, may be less likely to have large numbers of tuna associated with them, and may be more vulnerable to high kills-per-set due to the inexperience of younger dolphins. Also, the consistent underrepresentation of immature age classes in the spotted dolphin age distribution (Barlow and Hohn 1984) indicates that a very significant bias may occur in the sampling of immature animals. These are largely speculations, and until a well-supported explanation for sampling variability is presented and until some method of removing this bias is found, percent mature should not be used as an index of changes in spotted dolphin reproduction.

Gross Annual Reproductive Rate

Changes in GARR have been used as a measure of changes in the net rate of growth for a population (Smith 1983). This approach has been faulted on the basis that it does not consider age structure effects (Polacheck 1982), and more critically on the basis that such an approach is theoretically unsound (Goodman[7]). These criticisms do not, however, detract from the usefulness of GARR as an index of gross per capita reproduction for a population.

If GARR were robust to sampling conditions, it could be one of the most useful indices of population reproduction. One advantage is that a GARR index considers percent pregnant and percent mature simultaneously, and hence compensatory changes in these two do not affect the index. Simply stated, GARR is calculated as (the fraction of females in a population) × (the fraction of females that are mature) × (the fraction of mature females that are pregnant)/(gestation time). Unfortunately, percent mature is a major component in these calculations, and this parameter has been found to be dependent on sampling conditions. Until sampling problems associated with estimating percent mature are resolved, GARR is not likely to be a useful index of change in reproductive rates.

Between-Population Comparisons

The northern and southern stocks of spotted dolphins have been subjected to very different levels of fishing-related mortality. Smith[8] has estimated the northern stock to be at 38-55% of its 1959 level and the southern stock to be at 93-98% of its historical level. Density dependent increases in reproductive rates might be predicted for the northern stock relative to the southern stock.

The percentage of mature females that were pregnant differs significantly between the northern and southern stocks. Surprisingly, however, the southern stock was found to have the higher percent pregnant (36% vs. 33%). Another exploited population of spotted dolphins in the western Pacific was found to have an annual pregnancy rate of 0.254 (Kasuya 1976), which (with a gestation time of 11.2 mo) would give an average percent pregnant of about 24%. Considerable variability in percent pregnant can thus exist between spotted dolphin populations, none of which is obviously related to density compensatory effects. Sampling of the southern population has, however, been sporadic, and if annual variability in pregnancy rates is greater for that stock, a few years' data may not be sufficient to accurately estimate a long-term mean. Nonetheless, the tendency for a more exploited stock to have lower reproductive rates is worrisome, and future life history comparisons between the northern and southern stocks would probably be useful.

Evidence for density compensatory changes in pregnancy rates were also lacking when two spinner dolphin, *S. longirostris*, populations were compared (Perrin and Henderson 1984). They found similarly that the more heavily exploited stock (eastern spinners) had a lower percent pregnant than the less heavily exploited stock (whitebelly spinners). The opposite would be predicted based purely on density compensatory effects.

The overall percentage of pregnant females that are lactating is significantly higher for the northern spotted dolphins than for the southern stock. The biological significance of this result is questionable given the year-to-year variability in this parameter. Between-population comparisons of this percentage are not likely to be meaningful until the cause of this large annual variability is identified.

As was noted above, the percentage of females that

[7]Goodman, D. 1984. Uses of the gross annual reproduction rate calculation in the dolphin assessment. Admin. Rep. LJ-84-22C, 17 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[8]Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Admin. Rep. LJ-79-41, 120 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

are mature also appears to be higher in the southern stock than in the northern stock. Given the dependence of this parameter on sampling conditions, little confidence should be placed on this result. The direction of the difference (more immatures in the northern population) is consistent with a higher population growth rate in the north. Work is in progress to determine whether this difference could be due to differences in the age at sexual maturation (Myrick[9]).

No data exist yet on the mean age at sexual maturation for females in the southern stock. As mentioned in the Methods section, data do exist on the "length at sexual maturation" for both the northern and southern stocks. For the northern stock, this length appears to have increased from 176 cm in 1974 to 181 cm in 1983. For the southern stock this length was estimated as 175 cm from the pooled 1974-83 data. The length at sexual maturation is greater for the northern stock, which is consistent with the greater mean asymptotic length of the northern specimens (Perrin et al. 1979).

CONCLUSION

My intent in writing this paper was to identify indices that may be of value in monitoring the reproductive health of spotted dolphins in the eastern Pacific. Two of the indices that were examined (the percentage of mature females that are pregnant and the percentage of pregnant females that are lactating) are likely to be useful for this purpose. Both are relatively insensitive to sampling biases, and both measure important aspects of the female reproductive cycle. Problems exist in measuring the fraction of females that are mature. This parameter is also an important index of net reproduction in a population. It is possible that a stable index of percent mature could be obtained using some stratification scheme. A first approach might be to examine finer scale geographic differences in percent mature. Additional work is necessary before significance can be ascribed to between-population differences in percent mature.

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LITERATURE CITED

BARLOW, J., AND A. A. HOHN.
1984. Interpreting spotted dolphin age distributions. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-NMFS-SWFC-48, 22 p.

DIXON, W. J. (editor).
1981. BMDP statistical software. Univ. Calif. Press, Berkeley, 725 p.

FOWLER, C. W.
1984. Density dependence in cetacean populations. Rep. Int. Whaling Comm., Spec. Issue 6:373-379.

GAMBEL, R.
1975. Variations in reproduction parameters associated with whale stock sizes. Rep. Int. Whaling Comm. 25:182-189.

HESTER, R.
1984. Possible biases in the estimates of rates of reproduction in the spotted dolphins, *Stenella attenuata*. Rep. Int. Whaling Comm., Spec. Issue 6:337-341.

KASUYA, T.
1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Sci. Rep. Whales Res. Inst. 28:73-106.

LAWS, R. M.
1956. Growth and sexual maturity in aquatic mammals. Nature (Lond.) 178:193-194.

LOCKYER, C. H.
1972. The age of sexual maturity of the southern fin whale (*Balaenoptera physalus*) using annual layer counts in the ear plug. J. Cons. Int. Explor. Mer 34:276-294.

MIZROCH, S. A.
1983. Reproductive rates in Southern Hemisphere baleen whales. MS Thesis, Univ. Washington, Seattle, 103 p.

MYRICK, A. C, JR., A. A. HOHN, J. BARLOW, AND P. A. SLOAN.
In press. Reproduction in the female spotted dolphin, *Stenella attenuata*. Fish. Bull., U.S.

PERRIN, W. F.
1970. Color patterns of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). Zoologica (N.Y.) 54:135-149.

PERRIN, W. F., J. M. COE, AND J. R. ZWEIFEL.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

PERRIN, W. F., AND J. R. HENDERSON.
1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitations. Rep. Int. Whaling Comm., Spec. Issue 6:417-430.

PERRIN, W. F., R. B. MILLER, AND P. A. SLOAN.
1977. Reproductive parameters of the offshore spotted dolphin, a geographic form of *Stenella attenuata*, in the eastern tropical Pacific, 1973-75. Fish. Bull., U.S. 75:629-633.

[9]A. C. Myrick, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1984.

PERRIN, W. F., P. A. SLOAN, AND J. R. HENDERSON.
1979. Taxonomic status of the "southwestern stocks" of spinner dolphins, *Stenella longirostris*, and spotted dolphins, *S. attenuata*. Rep. Int. Whaling Comm. 29:175-184.

POLACHECK, T.
1982. The relationship between changes in gross reproductive rate and the current rate of increase for some simple age structured models. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-19, 9 p.

RASMUSSON, E. M., AND T. H. CARPENTER.
1982. Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. Mon. Weather Rev. 110:354-384.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eatern tropical Pacific. Fish. Bull., U.S. 81:1-13.

ANNUAL BAND DEPOSITION WITHIN SHELLS OF THE HARD CLAM, *MERCENARIA MERCENARIA*: CONSISTENCY ACROSS HABITAT NEAR CAPE LOOKOUT, NORTH CAROLINA

The presence of periodically repeating features in the preservable hard parts of various organisms allows scientists in several disciplines to make important inferences about the rates and timing of past events (Jones 1980; Rhoads and Lutz 1980). Analysis of growth lines deposited in shells of bivalve molluscs, for example, finds powerful application in the fields of paleontology (Rosenberg and Runcorn 1975), anthropology (Clark 1979), population ecology (Kennish 1980), and fisheries biology (Peterson et al. 1983). Possession of a reliable age marker in a bivalve shell enables fisheries biologists 1) to construct age-frequency distributions for various populations, which reflect the age-specific mortality rates and help permit estimates of sustainable yield, 2) to calculate individual growth rates and their variability among habitats, and 3) to understand age-specific reproductive schedules in exploited populations.

Unfortunately, the potential rewards in applying this aging technique have encouraged widespread use of growth line analysis prior to performing the necessary controls to test the annual periodicity of line deposition (Clark 1974; Gould 1979; Jones 1981). Because of the tremendous potential utility of this aging technique, we carried out mark-recapture tests of the annual nature of growth band deposition in shells of the commercially important hard clam, *Mercenaria mercenaria*, in a North Carolina sound (Peterson et al. 1983). Although these experiments provided convincing evidence that *M. mercenaria* deposits a reliable annual marker in the form of an internal summer growth band in its shell, this study was carried out in only a single locality in Back Sound, NC. Patterns of growth band deposition in bivalve molluscs may vary with environment on several scales: 1) over a broad geographic scale, *M. mercenaria* deposits summer bands in Back Sound, NC, and in Chesapeake Bay, but winter bands in all localities in northeastern states (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975; Clark 1979; Clark and Lutz 1982; Fritz and Haven 1983; Peterson et al. 1983); 2) among habitats within estuaries, *Protothaca staminea* appears to deposit unambiguous annual bands in muddy sand but not in a clean-sand habitat in Mugu Lagoon, CA (Peterson and Ambrose 1985); and 3) among nearby individuals within a single habitat, both *Chione fluctifraga* and *Protothaca staminea* from within the same restricted sample at Mugu Lagoon exhibit radically different patterns of daily line deposition (Hughes and Clausen 1980). We present here results of additional tests of the annual nature of internal growth band deposition in shells of *M. mercenaria* placed for 2 yr in several different field localities and estuarine habitats, in order to test whether our earlier (Peterson et al. 1983) demonstration of annual banding in North Carolina's *M. mercenaria* is robust to change in local habitat.

Materials and Methods

To extend the generality and power of our previous results, we designed a mark-recapture experiment to examine the frequency and clarity of band deposition in *M. mercenaria* at 5 additional sites (Fig. 1) within Carteret County, NC, near Cape Lookout. These sites were chosen to represent a wide geographic spread among several local water bodies, to permit contrasts between vegetated and unvegetated habitats, and to include more sandy (coarse) substrate than that in our original site. One site was selected on a fine sand flat in the North River about 12 km from our earlier Middle Marsh study site in Back Sound. Two sites were chosen about 38 km from Middle Marsh near the western end of Bogue Sound by the town of Cape Carteret: one on a fine sand flat and the other in a seagrass bed with mixed stands of *Zostera marina* and *Halodule wrightii*. The other two sites were situated in Core Sound about 6 km from Cedar Island Point and about 47 km from our initial Middle Marsh study site: one on a sand flat and the other in a *Halodule wrightii* meadow. All sites were on shallow subtidal bottom, accessible by wading and amenable to recovery of marked animals.

Table 1 summarizes the results of particle-size analyses done on duplicate surface (0-5 cm) sediment cores taken in August-September 1981 at each site to permit comparisons among the five new and one previous study sites. The five new sites are clearly characterized by having much coarser sediments than the previous study site but differ among themselves in sediment grade (Table 1). Contemporaneous

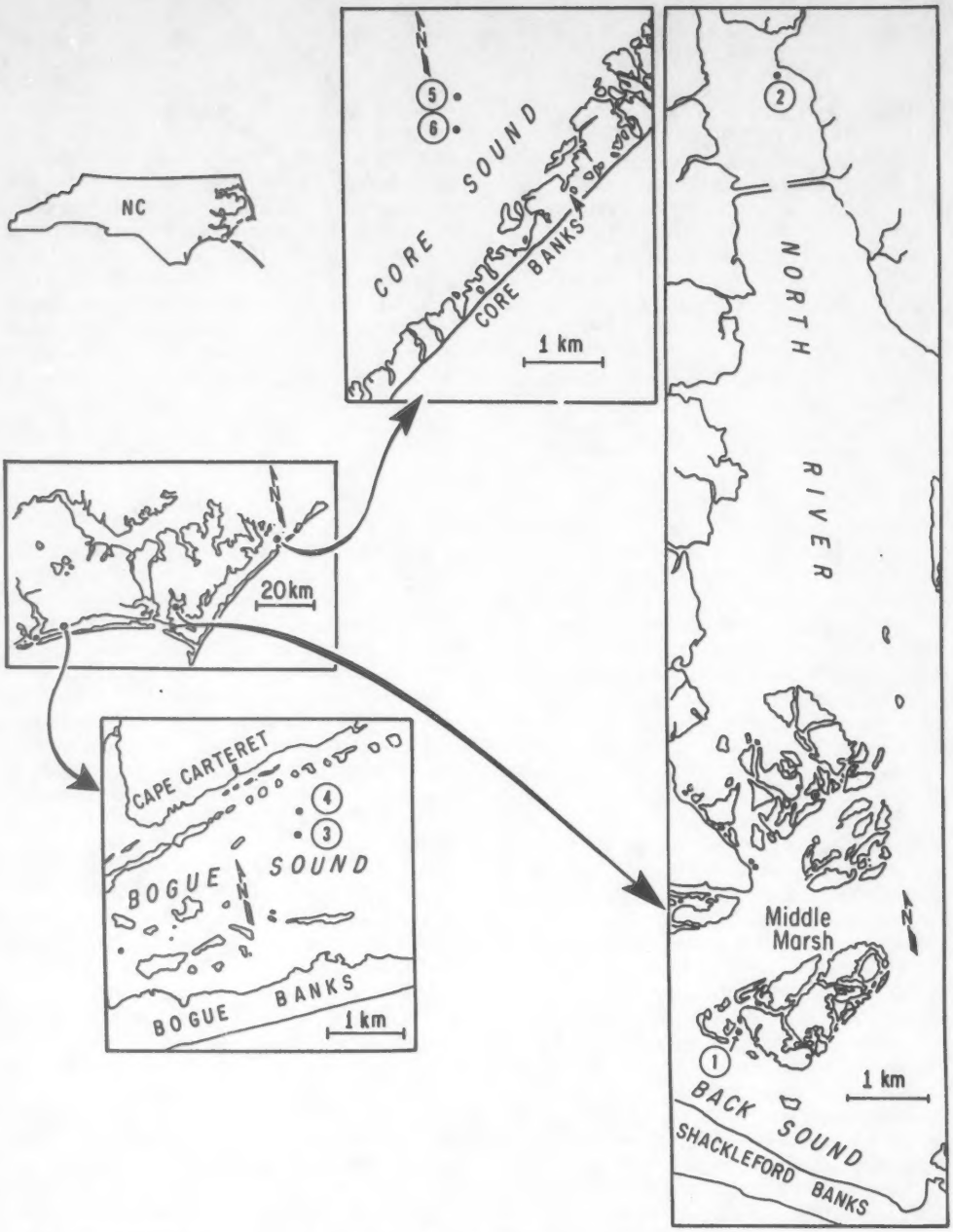

FIGURE 1.—Geographic locations of study sites (marked by dots near circled numbers) within North Carolina near Cape Lookout (marked by the arrow on the NC map): the previous site at Middle Marsh (1); new sites at North River (2); Bogue Sound sand (3) and seagrass (4); Core Sound sand (5) and seagrass (6).

TABLE 1.—Locations and sedimentary characteristics of the one previous (Middle Marsh) and five new study sites of *Mercenaria mercenaria*. Sedimentary data came from seiving and pipetting (Folk 1974) duplicate surface (0-5 cm) sediment cores taken in summer 1981 at each site. Percent silt-clay is percent of total sediment dry weight in fine (>4Φ) size classes.

Site	Location coordinates	Mean sediment parameters (±SD) Graphic mean	Percent silt-clay	Sorting coefficient
Middle Marsh in Back Sound	34°41′28″N 76°37′03″W	5.07 (0.28)	47.22 (12.24)	3.00 (0.51)
North River	34°48′22″N 76°36′48″W	2.35 (0.02)	2.97 (1.72)	0.61 (0.01)
Bogue Sound Sand	34°41′29″N 76°59′06″W	2.83 (0.09)	2.15 (0.05)	0.47 (0.02)
Bogue Sound Seagrass	34°41′36″N 76°59′05″W	3.05 (0.02)	9.31 (2.22)	0.95 (0.17)
Core Sound Sand	34°57′03″N 76°12′44″W	2.72 (0.07)	8.81 (2.03)	0.91 (0.16)
Core Sound Seagrass	34°56′59″N 76°12′43″W	2.40 (0.00)	3.10 (1.33)	0.60 (0.06

water temperature and salinity data are not available for all sites, but records from a variety of sources (Brett 1963; Thayer 1971; Williams et al. 1973; Sutherland and Karlson 1977; H. J. Porter, University of North Carolina, Chapel Hill, unpubl. data; W. Kirby-Smith, Duke University, unpubl. data) suggest that 1) water temperature patterns probably do not differ greatly across sites, with monthly averages ranging from winter minima of 2°-4°C to summer maxima of 29°-30°C, and 2) that salinities are slightly more variable across sites. Localities close to Atlantic Ocean inlets (Bogue Sound sand and seagrass sites and the previous Back Sound site at Middle Marsh) experience uniformly high salinities (30-36‰), except after severe rainstorms (Brett 1963; H. J. Porter, unpubl. data). Salinities in the upper portion of North River are only slightly lower because there is little freshwater inflow into that system (Thayer 1971). The lowest (22-28‰) and probably most variable salinities on a week-to-week scale occur at the two Core Sound sites, where exchange with the ocean is reduced and where any persistent north winds bring intrusions of low-salinity waters from Pamlico Sound (Williams et al. 1973).

At each of the five new study sites, we placed groups of 80 *Mercenaria mercenaria* in 1 m^2 field plots in late summer 1980, excavated them by hand in late summer 1981 to estimate growth and mortality and to replace missing and dead clams, and then finally recovered all living clams present in late summer 1982 (Table 2). All *M. mercenaria* used in these experiments were individually marked on the external shell surface with color-coded dots of Mark-Tex Corporation paints and measured initially and at both yearly samplings by calipers to the nearest 0.1 mm in each of three mutually perpendicular dimensions (length, height, thickness). Clams used in these mark-recovery experiments were chosen to reflect a size range from 1 to 10 cm in length. Before placing the marked and measured clams into the field plots, we first installed fences of 6 mm mesh plastic (VEXAR[1]) around the 1 m^2 plots. These fences were identical to those used and described previously (Peterson et al. 1983) and were designed to inhibit emigration and to mark off bottom plots to improve our ability to recover the marked clams. At the three unvegetated sites, we removed all initially present *M. mercenaria* and other large macrofauna before adding marked clams by first using fingers to plow systematically the top 10 cm of sediments and then twice systematically sieving in situ through 6 mm mesh the entire 1 m^2 surface to that same 10 cm depth. This procedure was not used at the initiation of the experiment at the two seagrass sites because it would have removed the seagrass itself. This same procedure was employed, although using a 3.2 mm mesh, at both yearly samplings to recover all marked clams from all 1 m^2 plots at each unvegetated site. At the two seagrass sites, marked clams were recovered by using a hydraulic suction dredge and collecting the contents of the top 15 cm on a 3 mm nylon mesh bag (see Peterson et al. 1983 for data on sampling efficiency of this device). Because of the removal of seagrasses, the locations of all seagrass plots were then shifted slightly (<3 m) to new, undisturbed positions for the second and final year.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Dates of experiment initiation and subsequent sampling of *Mercenaria mercenaria* for each of the five study sites.

Site[1]	Measuring dates 1980 initiation	1981 sampling	1982 termination
North River	6 August	30 July	2 August
Bogue Sound Sand	15 August	2 September	24 August
Bogue Sound Seagrass	15 August	24 August	24 August
Core Sound Sand	3 September	9 September	3 September
Core Sound Seagrass	3 September	11 September	3 September

[1]Each site held 1 m^{-2} enclosures of *Mercenaria mercenaria* at 80 m^{-2}; one enclosure contained clams derived from a common Back Sound site (supplemented by 10-20 mm clams from other Back Sound origins), and at least one other enclosure contained only locally derived clams.

At each site, all *M. mercenaria* in these experiments >20 mm in initial length came from one of two different sources. One enclosure at each site held clams planted at the constant density of 80 m^{-2} and collected initially from a single source, a seagrass bed along the southern shore of Back Sound (described in Peterson et al. 1984). One or two additional enclosures held clams collected locally at the specific study site, but again kept at the same 80 m^{-2} density. Low availability of clams in the 10-20 mm size class from the Back Sound source forced us to add hatchery-reared clams (spawned from Back Sound individuals) and wild-caught clams from Middle Marsh also in Back Sound to represent the 10-20 mm sizes in the "common source" enclosure at each site. This smallest size class was available locally at each site to complete the "local-origin" enclosures. This design was chosen to enable us to test whether there were any effects of clam origin (the single Back Sound source vs. local clams) at each of the five study sites.

Upon termination of the experiment almost exactly 2 yr after initial planting of the marked clams (Table 2), subsets of those clams that had survived the complete 2-yr period were selected from each origin treatment at each study site in as wide a range of sizes as possible. These clams were returned to the laboratory and killed by steaming. One valve from each of these 2-yr survivors was then sectioned, using a diamond blade on a slow-speed Buehler ISOMET saw, from umbo to ventral margin along the axis of greatest growth. The shell sections were sanded and polished when necessary to enhance the clarity of natural banding patterns. Because the initial size in August-September 1980 and the intermediate size 1 yr later were known for each of the marked individuals and could be marked on the shell surface, and because the marking and measuring process itself almost invariably induces deposition of a disturbance check which serves as a very precise internal shell marker (Peterson et al. 1983), we were then able to count with the unaided eye the number of additional growth bands deposited in the internal shell matrix of each clam during its final 2 yr of life. We also observed where these bands were deposited relative to the known sizes at the initial, intermediate, and final measuring dates. These observations permit a test of whether the reliability of using summer growth bands to age North Carolina's *M. mercenaria* varies with site (habitat) or clam origin in the vicinity of Cape Lookout.

Results

We sectioned shells from a total of 89 *M. mercenaria* collected alive in August-September 1982 and known by their paint codes to have been present in the field since the experiment's initiation 24 mo before (Table 2). Of these 89 individuals, 17 either exhibited insufficient growth to permit an accurate determination of the precise shell size at the experiment's initiation or else lacked a disturbance check to mark the precise size at initiation. Of the remaining 72 individuals, all but 2 deposited exactly 2 additional dark growth bands in the final 24 mo of life (Table 3). This pattern was consistent across all five study sites and did not change as a function of clam origin (Table 3). The appearance of the dark

TABLE 3.—For each of five new study sites: 1) numbers of hard clams cut for growth analysis from each origin treatment, 2) numbers of those with insufficient growth to assess band deposition accurately, 3) range of initial clam lengths for those clams with sufficient growth, and 4) average number of bands deposited in the 2-yr experimental period.

	Clam origin							
	Back Sound				Local site			
Study site	No. cut	No. with insufficient growth	Range in initial length (mm)	Av. no. of annual bands added in 2 yr (±1 SE)	No. cut	No. with insufficient growth	Range in initial length (mm)	Av. no. of annual bands added in 2 yr (±1 SE)
North River	10	1	19-74	2 (±0)	17	1	43-80	1.9 (±0.1)
Bogue Sound Sand	10	1	14-57	2 (±0)	11	2	21-72	2 (±0)
Bogue Sound Seagrass	3	1	39-69	2(±0)	3	1	44-48	2 (±0)
Core Sound Sand	10	0	18-75	2 (±0)	5	3	63-70	2 (±0)
Core Sound Seagrass	10	1	15-72	2 (±0)	10	6	46-56	2 (±0)

band in cross-section was identical to that previously described and illustrated by photograph (Peterson et al. 1983) of clams harvested from the Middle Marsh locality.

The pattern of band deposition relative to times of initial planting, first measurement (12 mo), and collection (24 mo) was also extremely consistent across all data sets. Initial planting in 1980 occurred during the period of annual band deposition for 70 of the 72 clams. (In one clam, the 1980 annual band was just completed and in another the 1980 annual band was just about to begin at the time of initial planting.) The disturbance check caused by the 12-mo measurement fell near the end of the growth band for 70 clams and just after the band for the two others. The time of collection in 1982 fell during or just immediately after the deposition of the 1982 annual band for all clams except those from local origin at North River. Of the 16 cut clams in that data set with sufficient growth for band resolution, 12 were just beginning to deposit their 1982 band at the time of collection (2 August, 3-4 wk earlier than the other sites—Table 2). Two of the 16 lacked the terminal band, whereas the remaining two had already deposited a substantial amount of the 1982 band. This North River local data set was the only one that contained any clams (only three) which had bands sufficiently faint to cause any doubt about recording them.

By counting all presumptive annual bands over the complete growth record of each clam, we also estimated the age of each of the 89 *M. mercenaria* used in this experiment. The estimated age at the experiment's initiation for the 17 clams excluded from our 2-yr tests ranged from 6 to 29 yr and averaged 15.5 yr (±1.7 SE). For the 72 clams that grew sufficiently and included a sufficient shell marker at initiation to be used in our 2-yr tests, age at experimental initiation ranged from 0 to 17 yr and averaged 3.9 yr (±0.3 SE). Thus, the average age of the clams that could not be used for our tests was significantly ($P < 0.01$ in a t-test) higher than that of the 72 clams that were used. Most (16 of 17) of the excluded clams lacked both sufficient growth and an obvious disturbance check at initiation. Only one clam was excluded with sufficient growth but without an adequate disturbance check. Although 16 clams lacked sufficient growth to determine accurately the shell size at the initiation of the experiment and were therefore excluded from our tests, all of these clams possessed discrete bands in their shells that could be counted separately. They were, however, close together at the terminal margin of the shell where separating them was not always possible and caused some uncertainty in their age estimates.

Discussion

Our banding data from recovery of marked and measured *M. mercenaria* after virtually 24 mo of terminal growth provide a compelling case for the reliability across different habitats of using major growth bands in sectioned shells to age hard clams in the Cape Lookout region of North Carolina. Our previous test of the annual periodicity of banding in North Carolina's *M. mercenaria* (Peterson et al. 1983) was carried out in only single locality, a Back Sound seagrass bed, characterized by almost equal proportions by weight of sands and muds in its surface sediments (Table 1). Through this study, we extend our tests of the reliability of annual band deposition in *M. mercenaria* to several additional sites, located in different bodies of water and characterized by much sandier sediments (Table 1). Of the six sites that we used for these tests, three were vegetated by seagrasses and three lacked macrophytic cover (Table 1). (Although our initial experiment in Middle Marsh was situated inside a seagrass bed, seagrasses were removed from the experimental plots during each sampling.) Despite these differences in local geographic location (and probably salinity), sediment grade, and seagrass presence, banding patterns were consistent and bands were deposited annually.

By using relatively high densities of 80 m^{-2} (over 10 times the average natural density found in a Bogue Sound seagrass bed by Peterson 1982, in North River, Bogue, Back, and Core Sounds by Beal 1983, and in Back Sound seagrass beds and sand flats by Peterson et al. 1984), we ran the risk of causing inhibition of growth. In fact, we were unable to analyze growth band deposition in 17 of our 89 clams largely because of insufficient growth in the terminal 2-yr increment. This problem may have been induced by our choice of relatively high density in these experiments, but it does have a natural analog. In areas with relatively slow growth and in older age classes where growth rate slows, aging North Carolina's *M. mercenaria* by counting annual bands in shell cross-section may be more difficult and lead to greater error than the consistency of banding results on our other 72 clams implies (Table 3). Nevertheless, banding even in these generally older clams that were excluded from our analyses was discrete and sufficient to permit us to estimate their ages. Aging does not appear to imply cessation of annual band deposition but only an increased dif-

ficulty in distinguishing one band from another.

Observations on the timing of annual band deposition in this study agree well with our previous results (Peterson et al. 1983). The 6 August-3 September period in 1980 consistently fell within the season of annual band deposition and near the end of the band at all five new study sites. Furthermore, the annual band was still being formed or had just been completed in all clams collected 24 August-3 September 1982. The banding of *M. mercenaria* in North Carolina appears to be a summertime event in contrast to the winter banding in northeastern populations (Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Clark and Lutz 1982).

The only clams that failed to deposit two additional annual bands in the 24 mo of this study were taken from the North River locals. This is also the only group that deviated in the timing of final band deposition relative to the 1982 collection date. Most of these clams had just initiated their 1982 bands at the time of collection in contrast to those from all other sites where 1982 band depositon was either far advanced or even terminated. This difference between sites is probably a consequence of the 3-4 wk earlier date of collection at North River (Table 2). Despite an identical, early collection date, the Back Sound clams transplanted to North River exhibited a pattern of band deposition in 1982 that more closely resembled the other four sites than did the North River local clams. This difference provides our only suggestion of an effect of clam origin, but we have no explanation for the possible effect and do not consider it a serious cause to doubt the consistency of annual band deposition in North Carolina's *M. mercenaria*.

The tests of consistency of annual band deposition across habitats in a local estuarine system provide an additional source of confidence in the accuracy of using internal banding patterns to age *M. mercenaria* in the Cape Lookout region of North Carolina. Concern over the lack of such controlled tests had earlier prompted Clark (1974), Gould (1979), and Jones (1981) to question the widespread assumption of regular periodicity in repeating shell features. Our demonstration of consistency in annual banding across local habitats should remove any doubts about the general applicability of using annual bands to age *M. mercenaria* in the Cape Lookout region of North Carolina. The variation in line deposition patterns which has been shown across habitats for *Protothaca staminea* (Peterson and Ambrose 1985) and among individuals within habitat for *P. staminea* and *Chione fluctifraga* (Hughes and Clausen 1980) does not exist for *M. mercenaria* near Cape Lookout. Our results will not only enable invertebrate fisheries biologists to use growth bands with confidence to age North Carolina's *M. mercenaria* but also should stimulate further research on understanding the environmental causes of variation in bivalve shell deposition patterns.

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Literature Cited

Barker, R. M.
1964. Microtextural variation in pelecypod shells. Malacologia 2:69-86.

Beal, B. F.
1983. Effects of environment, intraspecific density, predation by snapping shrimp and other consumers on the population biology of *Mercenaria mercenaria* near Beaufort, North Carolina. M.S. Thesis, Univ. North Carolina, Chapel Hill, 180 p.

Brett, C. E.
1963. Relationships between marine invertebrate infauna distribution and sediment type distribution in Bogue Sound, North Carolina. Ph.D. Thesis, Univ. North Carolina, Chapel Hill, 212 p.

Clark, G. R., II.
1974. Growth lines in invertebrate skeletons. Ann. Rev. Earth Planet. Sci. 2:77-99.
1979. Seasonal growth variations in the shells of recent and prehistoric specimens of *Mercenaria mercenaria* from St. Catherine's Island, Georgia. Am. Mus. Nat. Hist. Anthropol. Pap. 56:161-179.

Clark, G. R., II, and R. A. Lutz.
1982. Seasonal patterns in shell microstructure of *Mercenaria mercenaria* along the U.S. Atlantic coast. Geol. Soc. Am. Abstr. with Programs 14:464.

Folk, R. L.
1974. Petrology of sedimentary rocks. Hemphill Publ. Co., Austin, TX, 182 p.

Fritz, L. W., and D. S. Haven.
1983. Hard clam, *Mercenaria mercenaria*: Shell growth patterns in Chesapeake Bay. Fish. Bull., U.S. 81:697-708.

Gould, S. J.
1979. Time's vastness. Nat. Hist. 88(4):18-27.

Hughes, W. W., and C. D. Clausen.
1980. Variability in the formation and detection of growth increments in bivalve shells. Paleobiology 6:503-511.

Jones, D. S.
1980. Annual cycle of shell growth increment formation in two

continental shelf bivalves and its paleoecologic significance. Paleobiology 6:331-340.

1981. Repeating layers in the molluscan shell are not always periodic. J. Paleontol. 55:1076-1082.

KENNISH, M. J.

1980. Shell microgrowth analysis. *Mercenaria mercenaria* as a type example for research in population dynamics. *In* D. C. Rhoads and R. A. Lutz (editors), Skeletal growth of aquatic organisms: Biological records of environmental change, p. 255-294. Plenum Press, N.Y.

KENNISH, M. J., AND R. K. OLSSON.

1975. Effects of thermal discharges on the microstructural growth of *Mercenaria mercenaria*. Environ. Geol. 1:41-64.

PANNELLA, G., AND C. MACCLINTOCK.

1968. Biological and environmental rhythms reflected in molluscan shell growth. Paleontol. Soc. Mem. 2:64-80. [J. Paleontol. 42 (Suppl. to No. 5)].

PETERSON, C. H.

1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar. Biol. (Berl.) 66:159-170.

PETERSON, C. H., AND W. G. AMBROSE, JR.

1985. Potential habitat dependence in deposition rate of presumptive annual lines in shells of the bivalve *Protothaca staminea*. Lethaia 18:257-260.

PETERSON, C. H., P. B. DUNCAN, H. C. SUMMERSON, AND G. W. SAFRIT, JR.

1983. A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. Fish. Bull., U.S. 81:765-779.

PETERSON, C. H., H. C. SUMMERSON, AND P. B. DUNCAN.

1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. J. Mar. Res. 42:123-138.

RHOADS, D. C., AND R. A. LUTZ (editors).

1980. Skeletal growth of aquatic organisms: Biological records of environmental change. Plenum Press, N.Y., 750 p.

RHOADS, D. C., AND G. PANNELLA.

1970. The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3:143-161.

ROSENBERG, G. D., AND S. K. RUNCORN (editors).

1975. Growth rhythms and the history of the earth's rotation. John Wiley and Sons, Lond., 559 p.

SUTHERLAND, J. P., AND R. H. KARLSON.

1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Monogr. 47:425-446.

THAYER, G. W.

1971. Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N.C. Ches. Sci. 12:240-253.

WILLIAMS, A. B., G. S. POSNER, W. J. WOODS, AND E. E. DEUBLER, JR.

1973. A hydrographic atlas of large North Carolina sounds. Univ. North Carolina Sea Grant Publ. UNC-SG-73-02, 130 p. (U.S. Fish Wildl. Serv., Data Rep. 20, 130 p.)

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STANDING STOCK OF JUVENILE BROWN SHRIMP, *PENAEUS AZTECUS*, IN TEXAS COASTAL PONDS

The increased demand for timely information concerning management of shrimp stocks has renewed interest in developing reliable methods of predicting brown shrimp, *Penaeus aztecus*, crop size for the offshore Gulf of Mexico fishery. Advance information regarding shrimp abundance would also enable elements of the shrimp industry to prepare for a potentially good or poor harvest. Studies exploring the feasibility of predicting the annual abundance of brown shrimp off the Texas coast, initiated in 1960 (Baxter 1963), are based on the premise that postlarval and juvenile shrimp abundances are proportionally related to the subsequent commercial harvest (Berry and Baxter 1969).

A "good" predictor is one that is precise, timely, and cost effective. The abundance of postlarval shrimp as they move from the Gulf of Mexico into coastal bays is determined from semiweekly collections made by the National Marine Fisheries Service, Galveston, at the entrance to Galveston Bay between late February and early May (Baxter 1963). The postlarval shrimp index gives the earliest but least reliable indication of potential harvest. A more accurate but less timely prediction is derived from landings of the bait shrimp fishery. Statistics for bait shrimp landings since 1960 provide the basis for a predictive model developed by K. N. Baxter (Klima et al. 1982) defining the relationship between the bait abundance index and subsequent offshore catch. However, this prediction is not available until mid-June, just prior to the seasonal opening, because recruitment of brown shrimp into the bait fishery does not begin until May (Chin 1960). A third possible indicator is the standing stock size of juvenile shrimp in estuarine nursery areas measured before shrimp emigrate and become vulnerable to the bait fishery. This would provide an estimate earlier in the season than the bait index and may be a more accurate predictor than the postlarval abundance. Predictive capability increases with each successive life stage because of the decreased time span between the estimate and subsequent commercial harvest.

To examine the relationship between juvenile brown shrimp standing stock and offshore harvest, and to determine the suitability of juvenile brown shrimp abundance as a predictor, we conducted a mark-recapture study in Galveston Bay, TX, during the first week of June 1983. In this report we summarize the results of our study, compare estimates

obtained by mark recapture and an alternative drop sampler method, and discuss previously unreported results of 1970-71 studies (Welker and Baxter[1]).

Methods

Sydnor Bayou is a shallow coastal tidal pond in Galveston Bay (Fig. 1). The site was chosen because the single narrow entrance could be blocked easily with netting, thus preventing immigration and emigration of shrimp during the experiment, and because Sydnor Bayou was the site of a similar study in 1970.

The pond covers 32.4 to 36.4 ha, depending on the tide, is about 0.9 km long and 0.2 km at its widest point, narrowing to 6 m at the mouth. Maximum depth is about 1.5 m at high tide, with a 0.25 m tidal difference. Average salinity during the marking was 20.5 ppt and mean surface temperature was 28°C.

Weekly sampling of Sydnor Bayou with a 3 m otter trawl (25 mm stretched mesh) began 25 April 1983 to monitor the size of the juvenile shrimp. By 23 May 1983, most shrimp caught in the trawl were larger than the 40 mm TL (total length) minimum needed for tagging, and we decided to begin the mark-recapture experiment the next week.

Sydnor Bayou was blocked at dawn on 31 May 1983 across bridge B-1 (Fig. 1) with a 45.7 m net having a 6 mm mesh. The net was anchored to the bottom and remained in place for the duration of the experiment.

A 1.8 m diameter, 0.8 m deep round tank with continuous water flow and two 147 L aerated ice chests were set up on shore to hold shrimp during the marking process. Shrimp were caught in 49 5-min trawl hauls and transported to the marking site in aerated 45 L ice chests. To minimize marking mortality, only shrimp 40 mm TL and larger were marked and held in the large tank. Marking was accomplished by injection with pink fluorescent pigment as described by Klima (1965). Representative length-frequency, species-composition, and sex ratio information was obtained from shrimp captured in one trawl haul.

Marked shrimp were released within the hour after the target number (4,100) had been marked. Shrimp were scattered along the shallow grassy shoreline from moving skiffs. No dead or moribund shrimp were released, and release operations ceased whenever shore birds were attracted.

Four 61 cm × 61 cm × 20 cm wire cages, each containing 25 marked and 25 unmarked shrimp, were set out in the pond and remained submerged through all tidal stages. After 24 h, cages were raised and all shrimp, dead and alive, were counted, measured, and recorded for an estimate of marking mortality.

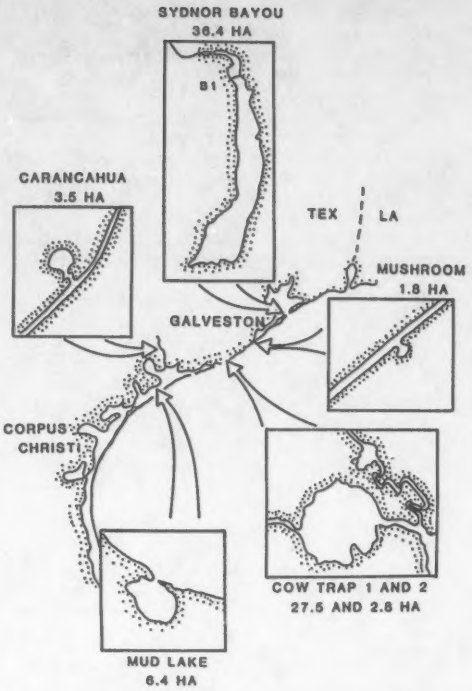

FIGURE 1.—Texas ponds selected for brown shrimp mark-recapture studies: Sydnor Bayou (1970 and 1983); Cowtrap, Mushroom, Carancahua, and Mud Lake (1971).

Recapture trawling began 18 h later, allowing marked shrimp time to distribute themselves in the unmarked population. For three consecutive days, all trawlable bottom was sampled by 5-min trawl hauls. Shrimp were returned to the laboratory where marked shrimp were identified under ultraviolet light. All marked and up to 100 unmarked recoveries were measured per tow. Length-frequency distributions for releases, marked recoveries, and unmarked recoveries are shown in Figure 2.

We estimated an initial population of juvenile brown shrimp using Bailey's (1951) modification of the Petersen formula

[1]Welker, W., and K. N. Baxter. Juvenile brown shrimp population estimates in Texas tidal marsh ponds. Unpubl. manuscr., 8 p. Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

$$N = M\frac{(C + 1)}{R + 1}$$

where M = number of marked shrimp released, corrected for marking mortality,
C = number of shrimp examined for marks,
R = number of recaptured marked shrimp in the sample.

The 95% confidence limits for the true population were estimated using the standard error of the large sample variance formula (Bailey 1951)

$$V(N) = \frac{M^2 (C + 1)(C - R)}{(R + 1)^2 (R + 2)}.$$

Application of this method is justified under the following conditions (Ricker 1975):

1) Marked shrimp suffer the same natural mortality as unmarked.
2) Marked and unmarked shrimp are equally vulnerable to fishing.
3) Marked shrimp do not lose their mark.
4) Marked shrimp become randomly distributed among unmarked.
5) All marks are recognized and reported on recovery.
6) There is not emigration or immigration occurring in the catchable population.

Results and Discussion

Overall marking mortality was 9%. One cage had unusually high mortality. Nineteen of 25 marked shrimp were alive at the end of 24 h, and the only evidence of the other 6 marked shrimp was pieces of exoskeleton. They apparently molted and were cannibalized. Holt (1982) suggested that the condition of shrimp prior to tagging dictates the survival of the tagged animals. When stressed animals were tagged, mortality more than doubled. Howe and Hoyt (1982) hypothesized that tags and marks may indirectly cause mortality by attracting predators. Farmer and Al-Attar (1979) found shrimp marked with subcutaneous pigment suffered high mortality (compared with controls) only when held with unmarked conspecifics. Clark and Caillouet (1973), however, found negligible marking mortality in a mark-recapture experiment with white shrimp, *P. setiferus*, when 50 marked and 50 unmarked control shrimp were held in a large pen in a pond rather than in several small cages. Costello and Allen (1962) stated that stained shrimp may be expected to survive at essentially the same rate as unmarked shrimp, regardless of presence of predators. To avoid overestimating marking mortality, we did not include the counts in the high cage in the calculation. The resulting 4% (3 dead marked shrimp out of 75) was similar to the marking mortalities of past studies in Sydnor Bayou, Mud Lake, and Mushroom (Welker and Baxter fn. 1).

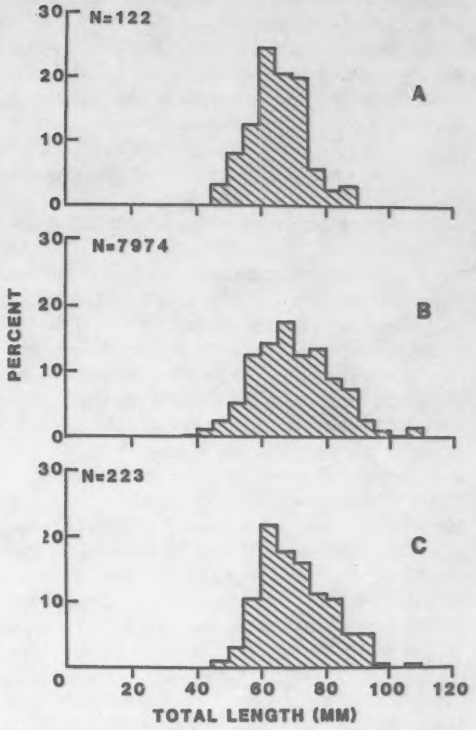

FIGURE 2.—Length-frequency distribution of brown shrimp in Sydnor Bayou, June 1983: A) representative sample of shrimp collected during marking; B) unmarked shrimp caught during recapture operations; and C) marked shrimp caught during recapture operations.

1983 Population Estimate

A total of 223 marked shrimp were among 12,304 shrimp caught in 94 recapture tows. Tides during the recovery period were low in the morning, approaching high tide in the afternoon. Areas along the shore and the south end of the bayou were shallow for trawling in the mornings, but could be adequately sampled in the afternoon. Distribution

of marked shrimp was random (one-sample runs test, $P = 0.960$; Siegel 1956).

The population estimate of 207,786 shrimp determined from mark-recapture data compared favorably with the results of a concurrent drop sampler experiment (Table 1). Shrimp densities were obtained using a 2.8 m^2 drop sampler at high tide. Detailed methodology has been described by Zimmerman et al. (1984). Drop samples were taken in two sets, four pairs each, in vegetated and nonvegetated areas, divided between the south and north ends of the bayou. Vegetated habitat was sampled along the bayou margins, while nonvegetated area sampling was in open waters of the bayou. Numbers of shrimp within the sampler were extrapolated to represent the shrimp population in the vegetated, nonvegetated, and total areas of Sydnor Bayou. Confidence intervals for the drop sampler were much wider than those for Petersen estimate because drop sampler estimates were based on a small number of samples. The drop sampler estimate for 36 ha was higher by about 92,000 shrimp. One reason for this difference is that the mark-recapture estimate reflects only that part of the population >40 mm TL, while the drop sampler measures density of small (<40 mm) shrimp more effectively, and these small shrimp are included in the estimate (Table 2). We calculated the drop sampler population estimate using only shrimp larger than 40 mm TL (Table 1). A chi-square test shows a significant difference between the drop sampler and mark-recapture size-frequency samples, categories 41-50 mm and higher ($\chi^2 = 109.45$, df = 6, P very small). The high chi-square value is due mainly to the greater number of 41-50 mm shrimp and the lower number of larger shrimp (81-90 mm), which may avoid the sampler, in the drop sample. Length-frequency composition of the drop sampler catch indicates that 23% of the 103 shrimp taken were smaller than 40 mm TL, while no shrimp smaller than 40 mm were captured by the otter trawl.

TABLE 1.—Sydnor Bayou brown shrimp population estimates determined by mark-recapture and drop sampler methods, June 1983.

Method	Estimated population	95% C.I.
Mark-recapture[1]		
32.4-36.4 ha	207,786	180,884-234,688
Drop sampler		
32.4 nonvegetated ha	185,000	41,900-479,000
4.0 vegetated ha	115,000	49,000-248,000
36.4 total ha	300,000	90,800-727,000
Drop sampler[1]		
32.4 nonvegetated ha	157,000	113,000-423,000
4.0 vegetated ha	88,000	53,500-183,000
36.4 total ha	245,000	166,000-606,000

[1]Estimate of shrimp population >40 mm TL.

TABLE 2.—Length-frequency composition of Sydnor Bayou brown shrimp samples taken with the otter trawl ($N = 8,197$) and drop sampler ($N = 83$), 1-3 June 1983.

Length (mm)	Otter trawl (%)	Drop sampler (%)
<20	0.0	9.7
21-30	0.0	1.9
31-40	0.0	11.7
41-50	3.8	19.4
51-60	17.3	19.4
61-70	32.2	22.3
71-80	25.7	12.6
81-90	16.0	1.9
91-100	4.2	0.0
>100	0.6	0.8

1970-71 Population Estimates

Our methodology for conducting a Petersen single census mark-recapture experiment with juvenile brown shrimp was developed during June and July 1971 studies of five Texas coastal ponds (Fig. 1). All ponds ranged from 0.3 to 0.9 m in depth during a normal summer tidal cycle. Cow Trap 1 and 2 had considerable emergent vegetation along their shorelines and were part of a large marsh complex. Extensive flooding of the marsh surrounding these ponds at flood tide greatly increased the area accessible to shrimp, but this shallow, vegetated area could not be sampled. Shrimp could move from pond to pond via flooded marsh and ditches, rendering block nets ineffective. Evidence of this movement was the netting of marked shrimp released in Cow Trap 1 and recaptured in Cow Trap 2. These problems precluded reasonable population estimates for the Cow Trap ponds, and large marsh complexes were avoided for future studies of this type.

Mud Lake, Carancahua, and Mushroom had generally well-defined shorelines, even during flood tide, and were not contiguous with other ponds or ditches. Mark-recapture methods were essentially the same as described for the 1983 study. Marking and holding operations were conducted on a portable barge rather than from shore (Emiliani and Marullo 1973). Population estimates determined by Bailey's (1951) formula ranged from 7,490 to 17,119 brown shrimp per hectare (Table 3). The lowest estimate was recorded in Mud Lake, where the highest percentage of total catch was <40 mm TL, while the highest estimate was for Carancahua. The density in Mushroom was close to that in Carancahua.

Although marking methods differed, a 1970 mark-

recapture study in Sydnor Bayou provided a population estimate for comparison. Marking was accomplished by spraying shrimp >40 mm TL with granular fluorescent pigment (Benton and Lightner 1972). Data analysis was as described for the 1983 Sydnor Bayou study. The average density of shrimp in Sydnor Bayou during the 1983 study was 37% of the May 1970 density and was the lowest per hectare estimate of any pond previously sampled (Table 3).

We believe that juvenile brown shrimp population density, determined by the mark-recapture method, may prove to be a good predictor of offshore production as we compile a longer term data base. Although the drop sampler (area-density method) may measure shrimp density more accurately, the Peterson mark-recapture method gives a more precise (having less variance) population estimate.

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Literature Cited

BAILEY, N. J.
1951. On estimating the size of mobile populations from recapture data. Biometrika 38:293-306.

BAXTER, K. N.
1963. Abundance of postlarval shrimp - one index of future shrimping success. Proc. Gulf Caribb. Fish. Inst. 15:79-87.

BENTON, R. C., AND D. LIGHTNER.
1972. Spray marking juvenile shrimp with granular fluorescent pigment. Contrib. Mar. Sci. 16:65-69.

BERRY, R. J., AND K. N. BAXTER.
1969. Predicting brown shrimp abundance in the northwestern Gulf of Mexico. FAO Fish. Rep. 57, 3:775-798.

CHIN, E.
1960. The bait shrimp fishery of Galveston Bay, Texas. Trans. Am. Fish. Soc. 89:135-141.

CLARK, S. H., AND C. W. CAILLOUET, JR.
1973. White shrimp (*Penaeus setiferus*) population trends in a tidal marsh pond. Mar. Fish. Rev. 35(3-4):27-29.

COSTELLO, T. J., AND D. M. ALLEN.
1962. Survival of stained, tagged, and unmarked shrimp in the presence of predators. Proc. Gulf Caribb. Fish. Inst. 14:16-19.

EMILIANI, D. A., AND F. MARULLO.
1973. Portable barge for estuarine research. Mar. Fish. Rev. 35(1-2):27-29.

FARMER, A. S. D., AND M. H. AL-ATTAR.
1979. Results of shrimp marking programmes in Kuwait. Kuwait Bull. Mar. Sci. 1:1-32.

HOLT, B.
1982. Short term mortality of tagged shrimp during field tagging experiments. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-97, 9 p.

HOWE, N. R., AND P. R. HOYT.
1982. Mortality of juvenile brown shrimp *Penaeus aztecus* associated with streamer tags. Trans. Am. Fish Soc. 111: 317-325.

KLIMA, E. F.
1965. Evaluation of biological stains, inks, and fluorescent pigments as marks for shrimp. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 511, 8 p.

KLIMA, E. F., K. N. BAXTER, AND F. J. PATELLA, JR.
1982. A review of the offshore shrimp fishery and the 1981 Texas Closure. Mar. Fish. Rev. 44(9-10):16-30.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y., p. 52-60.

ZIMMERMAN, R. J., T. J. MINELLO, AND G. ZAMORA.
1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt Marsh. Fish. Bull., U.S. 82:325-336.

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TABLE 3.—Summary of juvenile brown shrimp population studies in Texas coastal ponds.

Location	Start date	Number 5-min tows	Number shrimp caught	Percent <40 mm	Number marked and released	Percent released and recovered	Percent marking mortality	40+ mm population per hectare	95% confidence interval[1]
Sydnor Bayou									
32.4 ha	5/31/83	49	5,188	0.3	3,994	5.9	4.0	6,412	5,583-7,244
36.4 ha								5,709	4,970-6,448
Sydnor Bayou									
32.4 ha	5/21/70	32	8,045	—	7,718	1.7	4.0	17,933	14,198-20,042
36.4 ha								15,238	12,637-17,839
Mud Lake									
6.4 ha	6/3/71	27	6,750	20.0	6,120	10.8	4.0	7,490	6,956-8,025
Carancahua									
3.5 ha	6/7/71	26	6,301	7.0	4,574	9.8	8.0	15,697	11,815-17,087
Mushroom									
1.8 ha	7/2/71	24	8,348	6.0	4,142	28.8	4.0	14,375	13,628-15,120

[1]Bailey (1951) large sample variance.

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A POSSIBLE LINK BETWEEN COHO (SILVER) SALMON ENHANCEMENT AND A DECLINE IN CENTRAL CALIFORNIA DUNGENESS CRAB ABUNDANCE

Dungeness crab, *Cancer magister*, are taken commercially along the west coast of the contiguous United States from Avila, CA, to Destruction Island, WA (Fig. 1). During the early years of the California Dungeness crab fishery, effort was concentrated on the central California population which produced most of the state's landings (Fig. 2). The northern population subsequently became the major contributor to California's landings after an expansion of the fishery there during the 1940's.

Northern California landings (Fig. 2) generally have followed a fluctuating pattern similar to one expressed in Oregon and Washington; however, landings from the relatively isolated central California population failed to recover from a coastwide low during the early 1960's. The lower landings reflect a long-term reduction in abundance which has been variously attributed to egg predation by a nemertean worm *Carcinonemertes errens* (Wickham 1979) and to the effects of a long-term change in oceanic conditions (Wild et al. 1983).

The failure of the central California population to recover from the coastwide period of low abundance also occurred about the time coho salmon, *Oncorhynchus kisutch*, reared in Oregon and Washington hatcheries began to make a significant contribution to the west coast salmon fishery (Oregon Department of Fish and Wildlife 1982). The effect of salmonid predation on commercially important marine crustaceans has received little attention, although it is suspected that predation by salmonids introduced into a number of both small and large freshwater lakes (Nilsson 1972; Morgan et al. 1978) has substantially altered the abundance and species composition of their planktonic crustacean communities. Since numerous salmonid food habit studies (Heg and Hyning 1951; Petrovich 1970; Reilly 1983a) show that planktonic Dungeness crab megalops are a major component of the coho salmon diet, it is conceivable that an increase in the coho predation rate associated with an influx of hatchery coho into the central California region is at least partially responsible for the prolonged decline in Dungeness crab landings.

In this paper I first present evidence showing that a large portion of the coho salmon ultimately caught each summer off the west coast are in California waters during spring, the period Dungeness crab megalops are most abundant. I then compare and contrast survival indices to determine if the temporal variation in survival of both species is consistent with the predator-prey hypothesis.

Oregon Production Index Area Coho

Each spring and summer, a single coho salmon brood (year class) is recruited to the commercial salmon fishery off California, Oregon, and southern Washington, an area collectively referred to as the Oregon Production Index area or O.P.I. area (Oregon Department of Fish and Wildlife 1982). These fish entered the ocean to feed in May and June of the previous year, after having spent about 18 months in freshwater. Coho caught in the O.P.I. area before 1961 (Fig. 3) were predominately wild stocks. These stocks had declined to extremely low levels by 1960; however, the successful introduction of Oregon and Washington hatchery-reared coho resulted in a return to historical landing levels during the 1960's and 1970's. Much of the hatchery fish responsible for the increased landings are derived from early return Toutle River coho, which tend to enter fisheries south of their stream of origin (Hopley 1978).

Coho salmon made up only 10% or less of California's ocean salmon catch prior to the development of Oregon and Washington enhancement programs (Fry 1973). Most of these wild coho originated in the streams and rivers of Oregon and Washington (Allen 1965) and were landed primarily in the northern California ports of Crescent City and Eureka. The recruitment of hatchery fish increased the average annual coho contribution to 25% of the total ocean salmon catch, with the central California ports of San Francisco and Fort Bragg accounting for a considerably larger portion of the total coho catch.

FIGURE 1.—Commercial fishing areas for Dungeness crab off Washington, Oregon, and California. (Pacific Fishery Management Council (1979).)

Before 1973, the California salmon season (coho and chinook) opened on 15 April, although few coho were landed before June because of a minimum size restriction. As Oregon and Washington hatchery coho became available, a substantial increase in the hook and release of sublegal ("shaker") fish developed during the latter half of April to the middle of June. In an attempt to reduce the shaker problem, the season opening for coho was delayed until 15 May and the minimum size was reduced in 1973 (O'Brien and Lesh 1975).

California coho catches generally peak in July, then drop sharply in August, 2 mo before the salmon season closure. The midsummer decline is attributed to the northward exodus of fish returning to their natal stream to spawn (Fry 1973). It is however unclear when and by what route these fish entered California waters.

A general migration model (Loeffel and Forster 1970; Godfrey et al. 1975; Hartt 1980) proposes that newly emigrated west coast coho move immediately northward into the Gulf of Alaska, then during winter, undertake a southeasterly migration which brings them back into California, Oregon, and Wash-

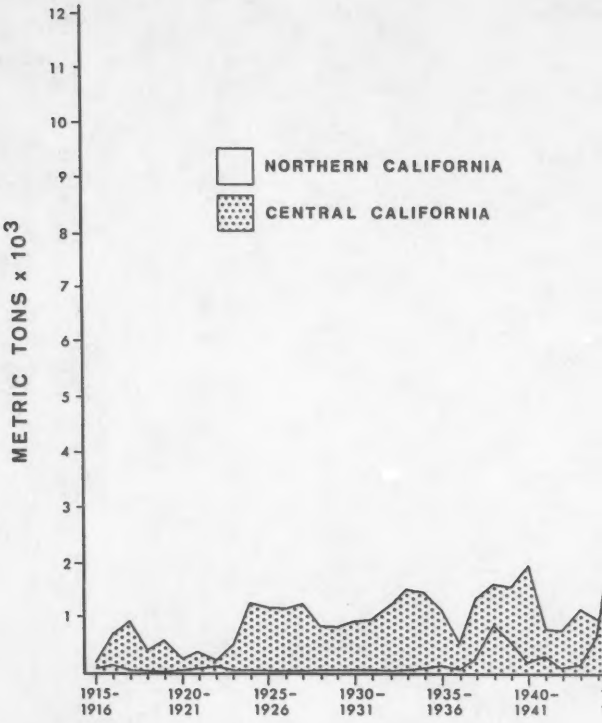
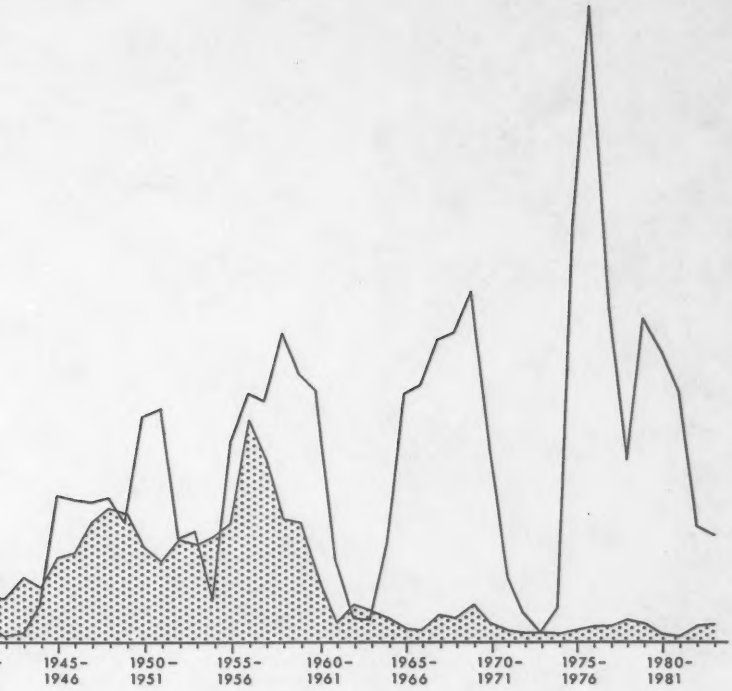


FIGURE 2.—Northern California (Crescent City, Eureka and Halfmoon Bay) commercial Dungeness crab landin



Eureka, Fort Bragg) and central California (Bodega Bay, San Francisco,
landings in thousands of metric tons, 1950-51 through 1983-84 seasons.

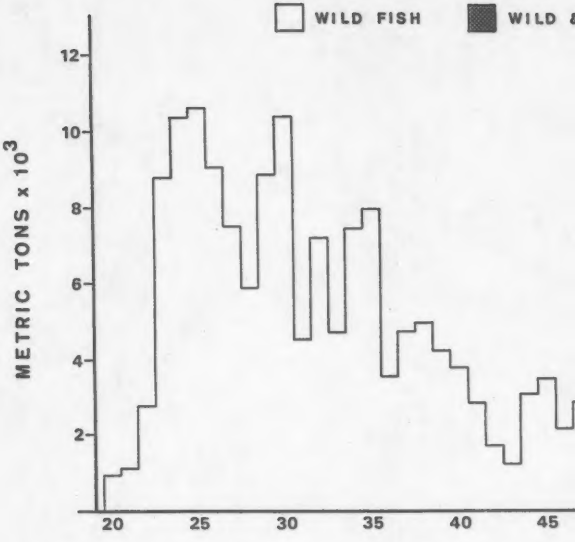
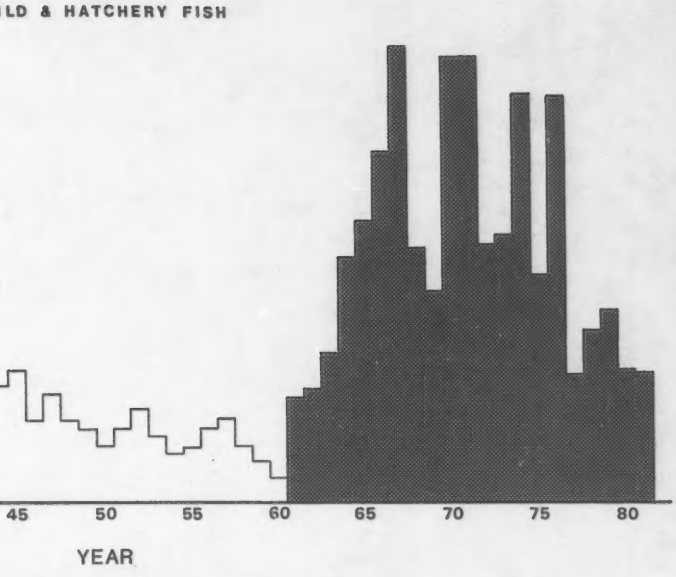


FIGURE 3.—Coho salmon landings in the Oregon Prod
tons. Figure adapted from Orego



n Production Index area, 1920 through 1981, in thousands of metric
Oregon Department of Fish and Wildlife (1982).

ington coastal waters each spring. Coho returning to the coast south of their natal stream would subsequently undergo the observed northward spawning migration. Each of these authors conceded however, that certain stocks or different portions of the same stocks may follow entirely different migratory routes. Scarnecchia (1981) felt that many coho produced along the west coast may either remain in adjacent coastal waters or move directly south after emigration from freshwater.

The dispersal pattern of 437 coho salmon tagged off northern California early in the 1971 and 1972 seasons clearly showed the northward movement of adult coho out of California (O'Brien 1973). Nearly all of the tagged fish recaptured in California were caught in May and June of each year while tagging was still being conducted. Oregon recoveries peaked in July and the first half of August, while most Washington recoveries occurred during the latter half of August through September.

California's share of the recaptured coho tagged off northern California (O'Brien 1973) was 9.3% in 1971 and 8.8% in 1972. These percent returns are very similiar to California's 13.0% and 8.3% share of the O.P.I. area catch in 1971 and 1972 respectively. Because, for practical purposes, one can assume that all of the coho caught in California originate to the north, the similarity between California's catch and tag returns would indicate that nearly all O.P.I. area coho stocks were off California during the tagging period. This supposition is extreme, but the results do suggest that a major portion of the coho ultimately caught in the O.P.I. area each year are in California waters during spring. The northward migration of large numbers of coho is further supported by the northward progression of peak monthly catches within the O.P.I. area (Pacific Fishery Management Council 1983), and the monthly catch distribution of hatchery marked coho (Hopley 1978).

Survival Indices Comparison and Discussion

Dungeness crab, unlike coho salmon, do not move any appreciable distance, therefore local landings are considered to be a good indicator of local abundance. In California seasonal landings are composed of at least three year classes, however northern California landings are generally dominated by 4-yr-old crab (Warner 1985), while central California landings, because of a faster growth rate, are dominated by 3-yr-old crab (Collier[1]).

An alignment of Dungeness crab seasonal landings with their dominant or "primary" year classes (Fig. 4) generates reasonably representive year class indices, if it is taken into consideration that extremely abundant year classes, such as the 1966 and 1972 year classes in northern California, probably dominate landings for more than 1 yr (Methot and Botsford 1982). The Dungeness crab year class indices (Fig. 4) suggest that a period of poor landings in both central and northern California during the early 1960's (Fig. 2) reflects poor survival of the 1958-60 year classes.

As mentioned earlier, northern California landings have been characterized by large seemingly cyclic fluctuations, the cause of which has been the subject of considerable research and debate (see Methot and Botsford 1982; Botsford 1984, for a review of this work). Of the hypotheses generated by these investigations, Wild et al. (1983) presented, in my opinion, the most tenable explanation for this particular period of low survival. They attributed the drop during this period to a reproductive failure caused by an unprecedented warming of coastal waters associated with the 1957 El Niño (the "warm water years" 1957-59, Radovich 1961).

The apparent recruitment of Dungeness crab to the northern California population of a "normal" year class in 1961 (Fig. 4), with the return of "normal" environmental conditions, ushered in several years of good survival. This recovery was not duplicated in the central California population, where a drop in the strength of the 1961 year class anteceded an extended period of poor survival. Wild et al. (1983) further proposed that a major change in the oceanic regime off central California is the primary cause of the continued poor survival there, although they do concede that ocean temperatures in certain years appear to have been favorable to Dungeness crab survival. Wickham (1979), on the other hand, suggested that the central California population has reached a new equilibrium, with worm predation now being the dominant biological control. It has yet to be proven which, if either, of these mechanisms is the primary cause of the continued poor survival in central California.

Alternatively, a direct comparison of O.P.I. catches with central California Dungeness crab year class indices (Fig. 5) illustrates a long-term inverse relationship which developed with the first recruitment of hatchery-reared coho salmon stocks in 1961. O.P.I. area landings are used to express the annual survival of coho potentially impacting central Califor-

[1]P. Collier, California Department of Fish and Game, 619 Second St., Eureka, CA, 95501, pers. commun. November 1984.

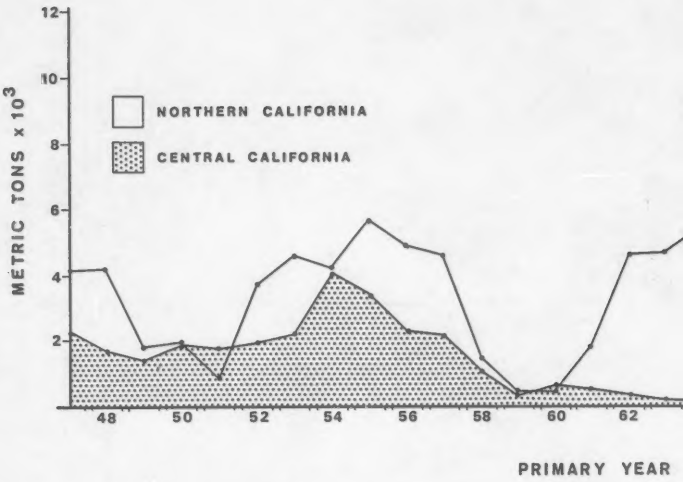
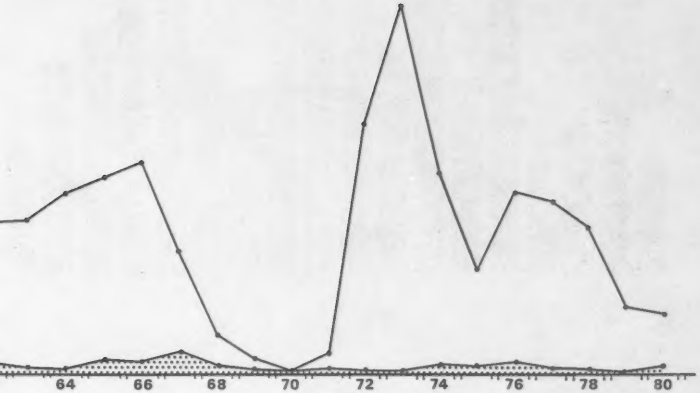


FIGURE 4.—Alignment of "primary" Dungeness crab year classes (1
lagged 3 yr in central California a



EAR CLASS

sses (1947-80) with the seasonal landings they dominate. Landings are
rnia and 4 yr in northern California.

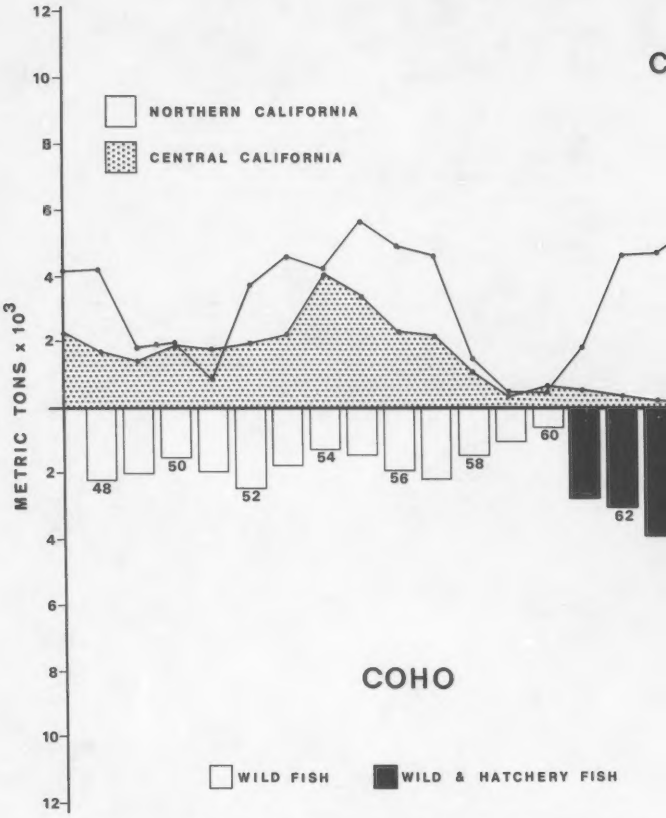
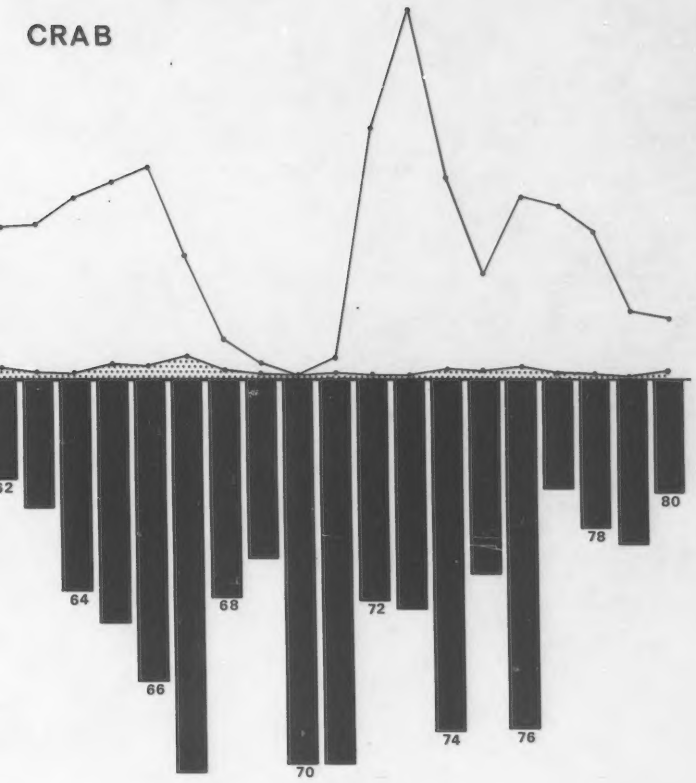


FIGURE 5.—Northern and central California Dungeness crab year
Production Index area coho



b year class indices (primary year classes) 1947-77, aligned with Oregon
a coho salmon landings, 1948-80.

nia Dungeness crab because of the evidence that California catch statistics underestimate the number of fish actually in the state during spring. These landings provide a straightforward measure of brood survival that is independent of distribution and local catchability.

Even though the relatively low O.P.I. area landings in 1961, 1962, 1963, 1977, and 1980 are comparable with the predecline era, the general pattern of correspondence in Figure 5 is consistent with an increase in the coho salmon predation rate on Dungeness crab megalops. Within the framework of the predator-prey hypothesis, the association of low O.P.I. area coho catches during the early years of the hatchery era with reduced Dungeness crab survival would indicate that a relatively small number of hatchery coho can effectively surpress megalops survival. This is particularly apparent when it is considered that hatchery production was at a minimum during the 1961-63 period and wild fish still dominated the catch (Oregon Department of Fish and Wildlife 1982).

The proposed impact of hatchery coho salmon on the Dungeness crab resource is best explained by the differences in the "functional response"[2] of wild and hatchery coho salmon. In controlled behaviorial experiments, Glova (1978) found that hatchery fry (43-88 mm) were largely nonterritorial, exhibiting a stronger tendency to aggregate than the wild fry. This behavioral pattern is believed to be the direct result of the unnaturally high densities found in hatchery operations. If adult hatchery coho retain this behavior, the tendency for Dungeness crab megalops to aggregate or "swarm" in coastal surface waters (Lough 1976) would theoretically make them more susceptible to predation (Eggers 1976). Also a reduction in the number of "search images" available to hatchery fish is believed to result in a more homogenous diet (Sosiak et al. 1979). Under these circumstances Dungeness crab megalops may become a more important component of the hatchery coho salmon diet.

The apparent good survival of the 1961-66 year classes in northern California (Fig. 5) suggests that the majority of the hatchery coho salmon produced during those years concentrated to the south of that population during the period when Dungeness crab megalops are most abundant. This supposition, together with recently acquired evidence that the central California Dungeness crab population is at least partially dependent on the recruitment of southward drifting megalops (Hatfield 1983; Reilly 1983b), further suggest that the theoretical predation zone critical to the central California population lies somewhere in the region of strong upwelling and high productivity between the two populations (Fig. 1). Not surprisingly, commercial fishermen have found coho salmon concentrated either before or early in the season in this region. The coho salmon stocks initally released during the early 1960's may possess an inate affinity for these waters.

Northern California landings of the Dungeness crab declined again during the 1970-71 season (Fig. 2). This period of low landings is apparently due to poor survival of the 1967-71 year classes (Fig. 5), which cannot be readily explained by an extended period of warmer than normal water. The various hypotheses to explain the northern California fluctuations notwithstanding, it is possible that hatchery-reared coho salmon began to limit Dungeness crab survival in northern as well as central California, concomitant with increased hatchery production[3] and/or environmental caused changes in distribution. There is some evidence from coho tagging that supports this supposition.

O'Brien (1973) reported that 17.3% of his returned tags were found in Oregon and Washington hatcheries during the 1971 season, whereas in 1972 only 3% were found in the hatcheries. An exceedingly strong 1972 Dungeness crab year class in northern California (Warner 1984) is in direct contrast with the very weak 1971 year class (Fig. 5) and is inversely related to the small number of tags found in hatcheries during the 1972 season. The small percentage of hatchery returns in 1972 suggest that there were fewer hatchery coho available for tagging in the northern California area during the 1972 season, and this could indicate relatively poor survival of hatchery fish throughout the O.P.I. area. It should be remembered that hatchery-reared coho theoretically have a much larger effect on Dungeness crab survival than wild fish.

Between 1972 and 1977 (Fig. 5), O.P.I. area coho survival and northern California Dungeness crab survival became more erratic. The association of relatively good Dungeness crab survival with good coho landings in 1974 and 1976 may, however, only indicate that coho were farther south than usual. McLain and Thomas (1983) showed that both 1973

[2]In predator-prey theory "functional response" is defined as the relationship between the rate at which individual predators consume prey and the density of that prey (Holling 1959).

[3]The number of hatchery-reared coho salmon released in the O.P.I. area increased from 7.5 million fish in 1960 to 60.8 million fish in 1981 (Oregon Department of Fish and Wildlife 1982).

and 1975 were years with an unusually weak California Countercurrent, or conversely, stronger than normal southward flow and cooler than normal coastal waters. If yearling coho do move directly into California waters after emigration from freshwater, then these anomalous conditions may have caused these fish to move farther south than usual, with the result that adult coho would have been south of the predation zone critical to the northern California Dungeness crab population in the spring of 1974 and 1976.

Since 1976 O.P.I. area coho landings have undergone an inexplicable decline in spite of increasing hatchery production. Theoretically, an increase in Dungeness crab survival should have accompanied this drop in coho survival. The drop in Dungeness crab survival, evident in Figure 5, is obviously inconsistent with the general theory but can be explained in two ways. First, it should be considered that the earlier O.P.I. area coho landings contained far fewer hatchery fish than those during the later years. It has been estimated that hatchery fish comprised 75% of the west coast coho catch by 1977 (Scarnecchia and Wagner 1980). Secondly, a coastal warming trend that began in 1976 (McLain 1983) may have resulted in a northward shift in coho distribution with a concomitant reduction in Dungeness crab megalops survival.

If coho have become the major limiter of Dungeness crab megalops survival within California, then the observed survival patterns suggest that a group of coho, possibly representing the original hatchery stocks, still experience consistently good survival and continue to move into the predation zone critical to the central California population. On the other hand, the more irregular Dungeness crab survival observed in northern California suggest that megalops survival there is more dependent on the vagaries of hatchery-reared coho distribution associated with environmental nuances.

Admittedly, most of the evidence used to support the predator-prey hypothesis is circumstantial. Nevertheless, three of the considerations presented —1) the fact that coho feed heavily on Dungeness crab megalops, 2) the evidence showing that many, if not most, Oregon and Washington hatchery coho are in California during the period megalops are most abundant, and 3) the coincidence of the extended central California Dungeness crab decline with a large increase in the number of hatchery coho within the O.P.I. area—suggest a possible relationship that deserves attention.

The capricious nature of predation on the early life stages of commercially important invertebrates undoubtedly contributes to the difficulties encountered when attempting to manage these relatively short-lived species on a sustained yield basis. If the hypothesized relationship between coho salmon and Dungeness crab eventually proves to be correct, then the salmonid enhancement process itself can be considered an experiment, offering insight into the role predators play in controlling the commercial abundance of many marine species.

Acknowledgments

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Literature Cited

ALLEN, G.
1965. Estimating error associated with ocean recoveries of fin-marked coho salmon. Trans. Am. Fish. Soc. 94:319-326.

BOTSFORD, L. W.
1984. Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41:99-107.

EGGERS, D. M.
1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. J. Can. Fish. Res. Board 33:1964-1971.

FRY, D. H., JR.
1973. Anadromous fishes of California. Calif. Dep. Fish Game, Resourc. Agency, 111 p.

GLOVA, G. J.
1978. Behavioral differences between wild and hatchery-produced coho salmon juveniles and their management implications. *In* B. G. Shepherd and R. M. J. Ginetz (Rapporteurs), Proceedings of the 1977 Northeast Pacific Chinook and Coho Salmon Workshop, p. 84-88. Can. Fish. Mar. Serv., Tech. Rep. 759.

GODFREY, H., K. A. HENRY, AND S. MACHIDORI.
1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm., Bull. 31:1-80.

HARTT, A. C.
1980. Juvenile salmonids in the oceanic ecosystem—the critical first summer. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 25-27. Oreg. State Univ. Press.

HATFIELD, S. E.
1983. Distribution of zooplankton in association with Dungeness crab, *Cancer magister*, larvae in California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource, p. 97-123. Calif. Dep. Fish Game, Fish Bull. 172.

HEG, R., AND J. VAN HYNING.
1951. Food of the chinook and silver salmon taken off the Oregon coast. Oreg. Fish. Comm., Res. Briefs 3(2):32-40.

HOLLING, C. S.
1959. The components of predation as revealed by a study of

small mammal predation of the European pine sawfly. Can. Entomol. 91:293-320.

HOPLEY, B. B.
1978. Genetic effects on Toutle-Cowlitz coho studies on the Columbia River. *In* B. G. Shepherd and R. M. J. Ginetz (Rapparteurs), Proceedings of the 1977 Northeast Pacific Chinook and Coho Salmon Workshop, p. 103-121. Can. Fish. Mar. Serv. Tech. Rep. 759.

LOEFFEL, R. E., AND W. O. FORSTER.
1970. Determination of movement and identity of stocks of coho salmon in the ocean using the radionuclide zinc-65. Oreg. Fish. Comm., Res. Rep. 2(1):15-27.

LOUGH, R. G.
1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-1971. Fish. Bull., U.S. 74:353-376.

MCLAIN, D. R.
1983. Coastal ocean warming in the northeast Pacific, 1976-1983. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific - A workshop, p. 61-86. Sponsored by the Cooperative Institute for Marine Resources Studies, Oregon State University, Sea Grant College Program, ORESU-W-83-001, Newport, OR.

MCLAIN, D. R., AND D. H. THOMAS.
1983. Year-to-year fluctuations of the California Countercurrent and effects on marine organisms. Calif. Coop. Oceanic Fish. Invest. Rep. 24:165-181.

METHOT, R. D., JR., AND L. W. BOTSFORD.
1983. Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39:1077-1083.

MORGAN, M. D., S. T. THREEKELD, AND C. R. GOLDMAN.
1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. J. Fish. Res. Board Can. 35:1572-1579.

NILSSON, N.-A.
1972. Effects of introductions of salmonids into barren lakes. J. Fish. Res. Board Can. 29:693-697.

O'BRIEN, P.
1973. An evaluation of the California troll silver salmon regulations. Calif. Dep. Fish Game, p. 1-12. (Mimeogr.)

O'BRIEN, P., AND E. W. LESH.
1975. Preliminary evaluations of the effects of California's new silver salmon troll regulations on the 1973 and 1974 troll seasons. Appendix 2 - Special report. *In* Pacific Marine Fisheries Commission, 27th Annual Report for the Year 1974, p. 49-53.

OREGON DEPARTMENT OF FISH AND WILDLIFE.
1982. Comprehensive plan for production and management of Oregon's anadromous salmon and trout. Part 2, Coho salmon plan. Oreg. Dep. Fish Wildl., var. pag.

PACIFIC FISHERY MANAGEMENT COUNCIL.
1979. Draft management plan for the Dungeness crab fishery of Washington, Oregon, and California. Portland, OR, 93 p.
1983. Proposed plan for managing the 1983 salmon fisheries off the coasts of California, Oregon, and Washington. An amendment and supplemental environmental impact statement to the "Fishery Management Plan for Commercial and Recreational Salmon Fisheries off the Coasts of Washington, Oregon, and California Commencing in 1978." Pacific Fisheries Management Council (526 S.W. Mill Street, Portland, OR), var. pag.

PETROVICH, A. A., JR.
1970. Biota of nearshore waters off Humboldt Bay and Trinidad Head 1960-1964, as shown by the diet of Pacific salmon. M.S. Thesis, Humboldt State Univ., Arcata, CA, 69 p.

RADOVICH, J.
1961. Relationships of some marine organisms of the northeast Pacific to water temperature. Calif. Dep. Fish Game, Fish Bull. 112:1-62.

REILLY, P. N.
1983a. Predation on Dungeness crabs, *Cancer magister*, in central California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource, p. 155-164. Calif. Dep. Fish Game, Fish Bull. 172.
1983b. Dynamics of Dungeness crab, *Cancer magister*, larvae off central and northern California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource, p. 57-84. Calif. Dep. Fish Game, Fish Bull. 172.

SCARNECCHIA, D. L.
1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Can. J. Fish. Aquat. Sci. 38:471-475.

SCARNECCHIA, D. L., AND H. H. WAGNER.
1980. Contribution of wild and hatchery-reared coho salmon, *Oncorhynchus kisutch*, to the Oregon ocean sport fishery. Fish. Bull., U.S. 77:617-623.

SOSIAK, A. J., R. G. RANDALL, AND J. A. MCKENZIE.
1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. J. Fish. Res. Board Can. 36:1408-1412.

WARNER, R. W.
1985. Age and growth of male Dungeness crabs, *Cancer magister*, in northern California. *In* Proceedings of the Symposium on Dungeness Crab Biology and Management, p. 185-187. Lowell Wakefield Fish. Symp. Ser., Univ. Alaska, Sea Grant Rep. 85-3.

WICKHAM, D. E.
1979. *Carcinonemertes errans* and the fouling and mortality of eggs of the Dungeness crab, *Cancer magister*. J. Fish. Res. Board Can. 36:1319-1324.

WILD, P. W., P. M. W. LAW, AND D. R. MCLAIN.
1983. Variations in ocean climate and the Dungeness crab fishery in California. *In* P. W. Wild and R. N. Tasto (editors), Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California resource, p. 175-188. Calif. Dep. Fish Game, Fish Bull. 172.

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THE EFFECTS OF NET ENTANGLEMENT ON THE DRAG AND POWER OUTPUT OF A CALIFORNIA SEA LION, *ZALOPHUS CALIFORNIANUS*

Interactions between pinnipeds and fisheries can be broadly divided into two categories: the role of pinnipeds on the mortality of commercially important fish species and the effect of commercial fisheries on the dynamics of pinniped populations. Although the former has received considerable attention (Hirose 1977; Fiscus 1979, 1980; Matkin and Fay 1980; DeMaster et al. 1982), the importance of the latter has been addressed only recently (Shaughnessy 1980; Fowler 1982; Scordino and Fisher 1983[1]).

Fishery interactions may affect pinniped stocks through changes in prey abundance, incidental takes, or entanglement in discarded fishing gear and plastic packing bands. Scordino and Fisher (fn. 1) have shown that the number of entangled northern fur seals, *Callorhinus ursinus*, on the Pribilof Islands, AK, has recently increased, and now comprises 0.4% of the harvested animals. Fowler (1982[2]) reviewed existing data concerning the accumulation of plastic litter on beaches of several Alaskan islands. Using the number of net fragments found on shore as a rough estimate of the size distribution of material adrift at sea, he concluded that at least 60% are larger than those measured on fur seals. Because most nets found on these animals weigh <600 g, a significant mortality undoubtedly occurs at sea from entanglement in larger fragments.

This paper evaluates the hydrodynamic effect of net entanglement and documents the behavior of an entangled animal. A California sea lion was trained to allow itself to become entangled in a twine trawl net fragment and the subsequent rise in drag was measured. Increased energy consumption and swimming power requirements associated with dragging net fragments were calculated from these measurements. The results provide an initial basis for assess-

[1]Scordino, J., and R. Fisher. 1983. Investigations on fur seal entanglement in net fragments, plastic bands and other debris in 1981 and 1982, St. Paul Island, Aiaska. Background paper submitted to the 26th Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 33 p.

[2]Fowler, C. W. 1982. Entanglement as an explanation for the decline in Northern fur seals of the Pribilof Islands. Background paper submitted to the 25th Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 24 p.

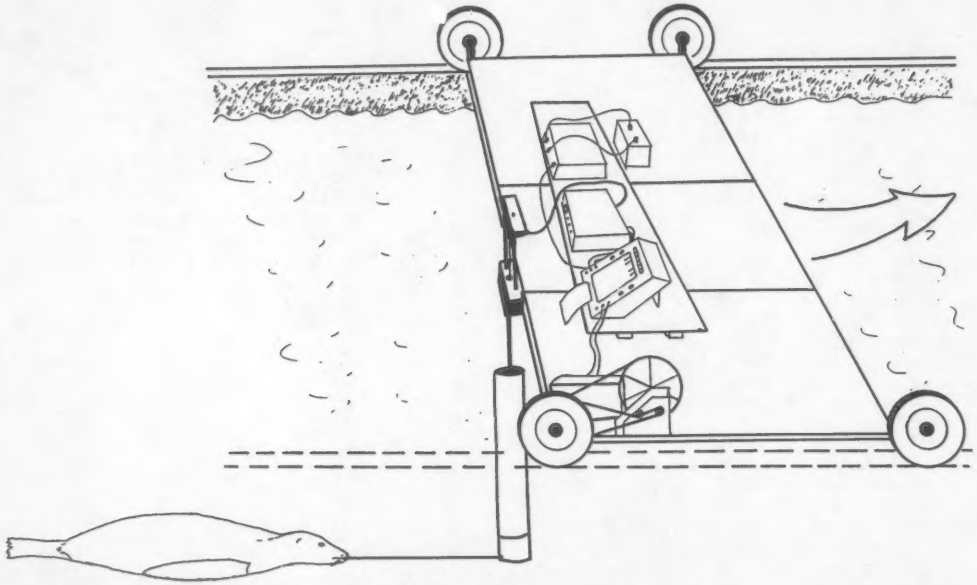

FIGURE 1.—Instruments and cart used in the drag experiments. The sea lion was towed passively underwater and the resultant force recorded. See text for further details.

ing the possible role of net entanglement on the mortality of pinnipeds at sea.

Materials and Methods

A female California sea lion, *Zalophus californianus*, was used in this work. The animal was kept in large seawater holding tanks at Scripps Institution of Oceanography. Its weight (45 ± 0.5 kg) remained constant throughout the course of this study, conducted during April 1983.

To measure drag, the sea lion was trained to bite onto a neoprene mouthpiece and be towed through the water behind a moving cart (Fig. 1). The cart, powered by a variable speed electric motor, travelled around a circular "ring" tank which had a depth of 3.5 m and inner and outer diameters of 14.5 and 21 m, respectively. A line was connected to the mouthpiece and the other end secured to a load cell (Western Scale Co.) which produced a voltage output proportional to the amount of tension on the line. The tow line extended down from the load cell, through a streamlined strut and around a teflon pulley attached to the end of the strut (Fig. 1). The pulley, enclosed by a streamlined fiberglass housing, was set at a depth of 1 m (>3 body diameters) to eliminate surface wave effects on drag (Hoerner 1959).

Drag was measured by continuously recording the signal output from the load cell during each towing session. The signal was amplified and recorded on a Brush[3] 220 strip chart recorder (Gould Instruments). At the end of each session, the load cell was calibrated using a hand-held dynamometer. A tachometer, attached to one of the outer cart wheels, was used to determine cart velocity. This was simultaneously recorded on the strip chart. The sea lion's velocity, while it was being towed down the middle of the tank, was computed using the speed of the outer wheel and the tank's circumference. After each experiment the data were smoothed by eye and drag and velocity determined. Only steady traces which varied less than ±3% were analyzed. Drag was then converted to newtons by multiplying the kilogram force reading of the load cell by the acceleration of gravity.

Once the sea lion's drag without a net was measured, the animal was trained to place its head through an opening cut in the mesh of a 1/8-in (3.2 mm) nylon twine trawl net. The opening was near the center of the net which measured 1.4 m × 5 m, with a stretched mesh size of 19 cm. The net had a dry weight of 580 g. After several trials, the sea lion became accustomed to the procedure and would allow itself to be towed with the net trailing from its neck. The net was removed after each session.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Drag on the sea lion, both with and without the net, increased with velocity (Fig. 2). This rise, however, was significantly greater when the animal was entangled, with the difference between the two curves increasing throughout the range of speeds. At the highest velocity of 3.5 m/s, the entangled drag was 111 N greater than that of the free animal (Table 1). Therefore, to maintain a cruising speed of 2.0 m/s an animal of this size, entangled in a net with similar hydrodynamic characteristics, would experience the equivalent drag of a free animal swimming at speeds above 4 m/s.

Power that the sea lion must expend for swimming can also be calculated from these measurements. Since drag is a force, power output (in watts) is a product of drag times swimming velocity (Webb 1975): P_0 = drag × velocity. Table 1 shows the results of such calculations and the effect of the net on the sea lion's required output.

Power output is a measure of the mean rate of energy expended by the swimming muscles at a given velocity (Webb 1975). It does not, however, reveal the total energetic requirements of the sea

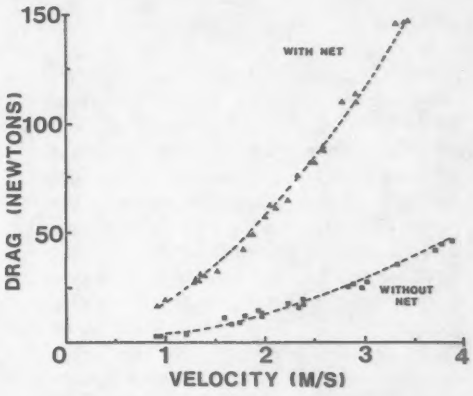

FIGURE 2.—Drag of a 45 kg sea lion with and withoug a net trailing from its neck. In both cases drag increased geometrically with speed. The regression equation with the net was 17.19 $vel.^{1.73}$, SEE (standard error of estimate) = 0.052. The equation for drag without the net was 2.93 $vel.^{2.06}$, SEE = 0.118.

TABLE 1.—The increase in drag and power output, and the estimated power input of the entangled sea lion. Drag with and without the net was calculated from the best fit regressions determined by the experiments. Power output was calculated by multiplying drag and the appropriate velocity. Weight specific power input is based on an efficiency (power out/power in) of 10%.

	Velocity (m/s)					
	1.0	1.5	2.0	2.5	3.0	.3.5
Drag (N)						
Without net	2.93	6.75	12.21	19.33	28.13	38.64
With net	17.19	34.66	57.01	83.87	114.97	150.11
Power output (W)						
Without net	2.93	10.13	24.42	38.65	84.40	135.24
With net	17.19	51.99	114.02	167.74	344.91	525.39
Power input (W/kg)						
Without net	0.7	2.3	5.4	8.6	18.8	30.0
With net	3.8	11.6	25.3	37.3	76.6	116.8

lion. Animals are not 100% efficient in converting metabolic energy to mechanical power needed for locomotion (Tucker 1975). Studies of penguins and fish which swim with their pectoral fins show that efficiency (power output/power input) varies between 5 and 15% (Webb 1973; Hui 1983). Female northern fur seals consume about 8 W/kg while at sea (Costa and Gentry in press). Using this number, the power output values estimated for the sea lion, and an assumed cruising speed of 2.5 m/s, an efficiency for fur seals of roughly 10% is obtained. Table 1 shows estimated energy requirements based on this efficiency for the sea lion with and without the net. Again it can be seen that to maintain a swimming speed of 2.5 m/s the sea lion would need to increase its metabolic expenditure by 50-fold, an impossibly high figure (Bartholomew 1977).

Discussion

There is little doubt that for an animal of this size, entanglement in a 600 g net will substantially increase its chance of mortality at sea. Drag, and hence the power required for swimming, is increased by the presence of a net. As a result, these animals will swim slower, at a greater energetic cost than free animals. Drag of the net, which rises geometrically with velocity, will prevent activities requiring high speeds as would be the case if such animals engaged in the pursuit of rapidly moving or evasive prey species. Additionally, migration or travel to and from the rookery will be energetically more costly. It is likely, then, that once an animal becomes entangled in net fragments of this size or larger, it enters a state of negative energy balance.

The animal's size as well as the size of the net plays an important role in the amount of drag experienced. A larger net will present more surface area to the water. Since drag is dependent on surface area (Vogel 1981), larger net fragments will result in greater drag. Similarly, if two different-sized animals are entangled in nets of the same dimensions, the smaller will experience a larger relative increase in its drag and power requirements. If animals of different age classes encounter net fragments with equal probability, it is expected that the younger age classes will suffer a proportionally higher mortality.

Although starvation is undoubtedly the long-term result of net entanglement, other factors may have a more immediate effect. This was particularly evident during an observation of an actual entanglement. In the initial training phase of the sea lion, a net with a larger mesh size was used. At one point, while the net was floating in the water, the sea lion swam up from below and inserted its head through one of the mesh openings. Upon sensing the net around its neck it gave a strong backwards stroke, trying to retract its head. The backward movement brought some of the trailing net in front of it and when the animal then swam forward and dived underwater, another strand slipped onto its neck. This caused a violent reaction with the sea lion twisting and thrashing wildly. The twisting further entangled the animal and tightened the net. Within 1½ to 2 min the animal was completely entangled with three or four loops of mesh tight around its neck.

The net was so tight that an observer on the side of the tank was unable to pull it from the sea lion's head, and it was necessary to drain the holding tank. During this time, the animal swam around the tank barking and often thrashing about while trying to bite the net. This appeared to further tighten the net which, when finally removed, was so tight that a finger could not be slipped between the net and the animal's neck.

If the behavior of otariids at sea is similar to that exhibited by the entangled sea lion, then drowning may be another more immediate cause of mortality. Twisting and rolling could foul the foreflippers and prevent the animal from swimming. This seems particularly likely if it became caught in a larger net. Additionally, because the net was so tightly wrapped around the sea lion's neck, necrosis of the skin tissue and an open wound may have occurred within a matter of hours to a few days. Constant swimming could continue to tighten the net. Although several authors (Scordino and Fisher fn. 1) have speculated that neck wounds indicate a period of entanglement longer than 4 mo, these observations suggest that beached animals with open wounds may have become tangled only a few days prior to sighting.

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Literature Cited

BARTHOLOMEW, G. A.
1977. Energy metabolism. *In* M. S. Gordon (editor), Animal physiology: Principles and adaptations, p. 57-110. Macmillan Publ. Co., N.Y.

COSTA, D. P., AND R. L. GENTRY.
In press. Free ranging energetics of northern fur seals. *In* R. L. Gentry and G. L. Kooyman (editors), Fur seals: Maternal strategies on land and at sea. Princeton University Press.

DEMASTER, D. P., D. J. MILLER, D. GOODMAN, R. L. DELONG, AND B. S. STEWART.
1982. Assessment of California sea lion fishery interactions. Trans. N. Am. Wildl. Nat. Resour. Conf. 47:253-264.

FISCUS, C. H.
1979. Interactions of marine mammals and Pacific hake. Mar. Fish. Rev. 41(10):1-9.
1980. Marine mammal-salmonid interactions: a review. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific Ocean, p. 121-131. Oregon State Univ. Press, Corvallis.

FOWLER, C. W.
1982. Interactions of northern fur seals and commercial fisheries. Trans. N. Am. Wildl. Nat. Resour. Conf. 47:278-292.

HIROSE, P.
1977. Incidence of seal-damaged salmonids sampled from the lower Columbia river gillnet fishery, 1972-1976. Oreg. Dep. Fish Wildl., Inf. Rep. 77-4, 6 p.

HOERNER, S. F.
1959. Fluid-dynamic drag. Practical information on aerodynamic drag and hydrodynamic resistance. [Published by the author.] Midland Park, N.J. 416 p.

HUI, C. A.
1983. Swimming in penguins. Ph.D. Thesis, Univ. California, Los Angeles, 185 p.

MATKIN, C. O., AND F. H. FAY.
1980. Marine mammal-fishery interactions on the Copper river and in Prince William Sound, Alaska, 1978. Final Report to U.S. Marine Mammal Commission for contract MM8AC-013, 71 p. Publ. No. PB80-159536, Natl. Tech. Inf. Serv., Springfield, VA.

SHAUGHNESSY, P. D.
1980. Entanglement of Cape fur seals with man-made objects. Mar. Pollut. Bull. 11:332-336.

TUCKER, V. A.
1975. The energetic cost of moving about. Am. Sci. 63:413-419.

VOGEL, S.
1981. Live in moving fluids: The physical biology of flow. Willard Grant Press, Boston, MA, 352 p.

WEBB, P. W.
1973. Efficiency of pectoral-fin propulsion of *Cymatogaster aggregata*. *In* T. Y.-T. Wu, C. J. Brokaw, and C. Brennen (editors), Swimming and flying in nature, Vol. 2, p. 423-1005. Plenum Press, N.Y.
1975. Hydrodynamics and energetics of fish propulsion. Fish. Res. Board Can. Bull. 190, 158 p.

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NOTES ON THE LIFE HISTORY OF THE CATSHARK, *SCYLIORHINUS MEADI*

The catshark, *Scyliorhinus meadi* (family Scyliorhinidae) is a rare, poorly known species, easily identified by the eight dark saddle-like blotches along the dorsal surface. Springer (1966) first described *S. meadi* and Springer and Sadowski (1970) assigned it to subspecies status of *S. retifer*. In Springer's (1979) revision of the family, it was again given species status. At present only 10 immature specimens of *S. meadi* have been collected, seven males (180-490 mm in length), two females (235 and 385 mm in length), and one 190 mm specimen of unknown sex. This paper reports on the collection of an additional specimen of *S. meadi* and provides valuable life history information.

During a cruise aboard the RV *Delaware II* on 5

May 1984, a specimen of *S. meadi* was collected at a depth of 412 m using a 17 m otter trawl at lat. 28°59.85'N, long. 79°55.98'W. The shark measured 430 mm in length and weighed 0.4 kg. This shark, together with its stomach contents, is deposited at the Ichthyological Museum of the Florida Department of Natural Resources, St. Petersburg (FSBC 16208). Examination of the reproductive system revealed a developing right ovary measuring 4.4 cm long and 0.6 cm wide. The left ovary was atrophied. Follicles teased from the right ovary measured 0.75 mm in diameter. The nidamental glands were 3.0 mm wide and 8.0 mm long. The oviduct, from nidamental gland to vagina, was 82 mm long and 1.0 mm wide. Gut content examination revealed several cephalopod beaks and tentacles, shrimp remains, and the articulated caudal skeleton from a relatively large, unidentified teleost.

This specimen of *S. meadi* is the third and largest female collected to date. Burgess et al. (1979) reported on the collection of a 385 mm total length female in which the right ovary measured 33.2 mm and the left 8.9 mm in length. This represents about 8.6% of the total length of the shark. The right ovary of the specimen reported in this paper represents about 10.2% of the shark's total length. This specimen is immature, but the allometric increase in ovary length, and the fact that the left ovary was completely atrophied suggests that the specimen might be considered a subadult (maturation begun). The small size of the Florida Bahama specimens compared with the North Carolina examples led Burgess et al. (1979) to suggest geographical size segregation. This large specimen from off the central Florida east coast does not support this segregation. Discovery, in gut content examination, of the large, teleost caudal skeleton suggests an unexpected ability to prey on relatively large fishes.

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Literature Cited

BURGESS, G. H., G. W. LINK, JR., AND S. W. ROSS.
1979. Additional marine fishes new or rare to Carolina waters. Northeast Gulf Sci. 3(2):74-87.

SPRINGER, S.
1966. A review of western Atlantic cat sharks, Scyliorhinidae, with descriptions of a new genus and five new species. U.S. Fish. Wildl. Serv., Fish. Bull. 65:581-624.
1979. A revision of the catsharks, Family Scyliorhinidae. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Cir. 422, 152 p.

SPRINGER, S., AND V. SADOWSKY.
1970. Subspecies of the western Atlantic cat shark, Scyliorhinus retifer. Proc. Biol. Soc. Wash. 83:83-98.

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A COMPARISON OF SCALE AND OTOLITH AGING METHODS FOR THE ALEWIFE, *ALOSA PSEUDOHARENGUS* [1]

Beginning in 1971, the Maine Department of Marine Resources monitored the harvests of anadromous alewives ascending the Damariscotta River (Libby 1982). Part of this monitoring assessed changes in age composition within and between years. Aging was done by interpreting the number of scale annuli in terms of fish age as has been done in earlier investigations (Havey 1961; Rothschild 1963; Marcy 1969). However, scale annuli were sometimes difficult to interpret, so in 1979, methods for removing and reading alewife otoliths were studied. A relatively fast and efficient method was developed for removing otoliths. The ease with which the otoliths were processed to age fish prompted an analysis of which method (scales or otoliths) was best for determining the age of an alewife. This paper compares the precision of reproducibility and accuracy between the scale and otolith methods.

Materials and Methods

Alewives, *Alosa pseudoharengus*, were taken daily from the commercial harvest throughout the fishing period for their otoliths and scales. The fish were taken to the laboratory, sexed, and measured for length and weight. About 10 scales were removed from the left side above the lateral line just posterior to the dorsal fin. The scales were cleaned and put into envelopes labeled with the length and sex of the alewife. In 1963, Rothschild described the alewife scale and characteristics of the annuli.

Otoliths were collected and stored as follows: A

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 89-304, as amended, Commercial Fisheries Research and Development Act, Project AFC-21-1.

transverse cut was made at the point of attachment of the operculum, which severed the head leaving some attachment of skin to the body. The head was then pulled away from the body removing the gills, leaving the skull clear of the gills and viseral blood. When time did not permit for further processing, all the heads from a day's sample were placed onto a tray and frozen for later analysis. For otolith removal, the head was held ventral side up and a transverse cut was made into the skull at the point of dorsal musculature attachment (Fig. 1a). A correct cut was sliced through the ends of the semicircular canals containing the sagitta otolith (Fig. 1b). Kornegay, in 1978, described the sagitta otolith that is used for age determination of the alewife.

Each otolith was extracted with microforceps, placed on absorbent paper, and rubbed lightly to remove any adhering tissue. After drying, otoliths were placed in depressions in black Plexiglas[2] trays and covered with Permount (see Libby 1982). Williams and Bedford (1974) described the growth and collection of otoliths and interpretation of otolith annuli in general. The Atlantic herring, *Clupea harengus*, otolith which is similar to the alewife otolith, was described by Watson (1964). He reported on the high validity of its use for aging and the high reproducibility of readings between readers.

Scales and otoliths were collected from 536 fish. Thirty-one fish were discarded because the otoliths or scales were unreadable or the shape of the otolith revealed that the fish was a blueback, *A. aestivalis*. Price (1978) explained the difference in otolith morphology between the two species. A final count of

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 1.—a) Ventral side of head of *Alosa pseudoharengus*. Dark line shows musculature attachment to the skull where transverse cut is made. b) Section of skull cut away showing posterior ends of the semicircular canals containing the sagitta otoliths.

505 alewives was used for the analysis. Otoliths and scales were read using a binocular dissecting scope at 30×-60×.

Each otolith and scale for an age shown in Figure 2 was collected from the same fish. The otoliths were taken from the left side of the head and each scale was chosen for the best annuli appearance of all scales from that fish. The scale annuli shown are at the anterior portion of the scale that is normally covered by surrounding scales. The otoliths were photographed with a 35 mm camera mounted on a microscope at 11×.

Aging was done independently by two people (readers; subsequently referred to as R_1 and R_2). Ages derived from scales and otoliths by each reader were referred to as an age set. Scales and otoliths were read without knowledge of fish length or sex. A true age was established for each fish by reexamining scales and otoliths together with length and sex. The five age sets were compared to show 1) the precision of aging reproducibility (measurement of how close the ages are for two or more readings); and 2) the aging accuracy (age determinations compared with the true age).

Three analyses were used to evaluate precision and accuracy. Percent agreement (PA) compared two to three age sets to reveal what portion of the fish were aged alike between age sets. An index of average percent error (APE) developed by Beamish and Fournier (1981) was used to show the degree of variation between age sets. APE is expressed as

$$\frac{1}{N}\sum_{j=i}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right]$$

where N is the number of fish aged; R is the number of ways each is aged; X_{ij} is the ith determination of

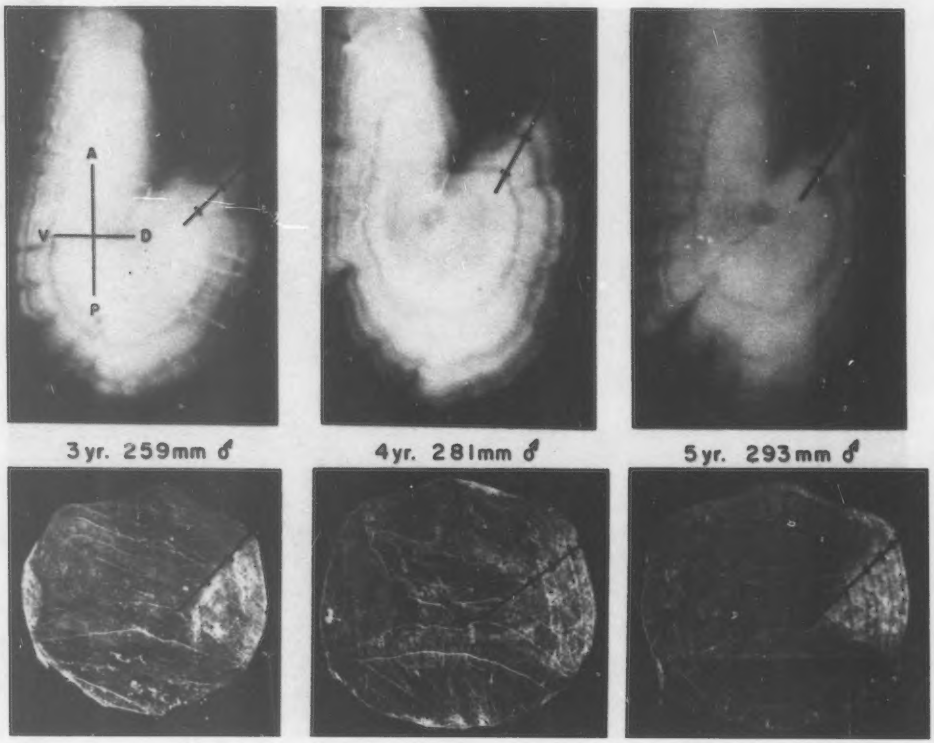


FIGURE 2.—Gross comparisons of otoliths and scales of alewives from ages 3 through 7. The otolith and scale were taken from the same fish for each age. The age-3 otolith shows: A - anterior; P - posterior; D - dorsal; and V - ventral orientation of the otoliths

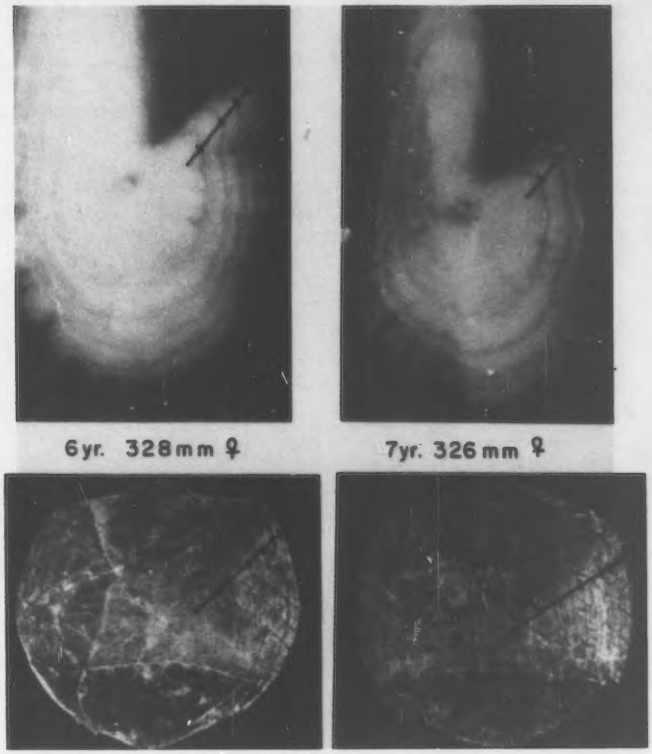
the jth fish; the X_j is the mean age calculated for the jth fish. The third method used the mean coefficient of variation (V) (Chang 1982). This was an alternative index to APE that provided a statistical test of reproducibility between agings. The coefficient was a measure of the standard deviation between all ages of fish divided by the mean age. The sum of the coefficients was then divided by the number of fish aged. PA, APE, and V are all expressed as percents.

The difference between PA and APE or V is that the former measures the actual agreement between age sets and the latter measures the amount of variation between age sets. Two treatments (a treatment was the comparison of two or more age sets) that had the same PA values might have differing degrees of variation and therefore different values of APE or V. The smaller the APE or V values, the less variation there was between age determinations.

Values for PA, APE, and V were computed for 10 treatments: scales vs. otoliths from R_1; scales vs. otoliths from R_2; scales from R_1 vs. R_2; otoliths from R_1 vs. R_2; scales from R_1 and R_2 vs. true age; otoliths from R_1 and R_2 vs. true age; male scales from R_1 vs. R_2; female scales from R_1 vs. R_2; male otoliths from R_1 vs. R_2; and female otoliths from R_1 vs. R_2. Treatments were also compared as to the relative sizes of the PA, APE, and V values.

Results

Figure 2 compares the physical appearance of otoliths and scales for ages 3 through 7. The photograph of the age-3 otolith shows its orientation as it lies in the sacculus. The dorsal side, including the anti-rostrum, shows the best contrast between the light opaque (summer growth) regions and the dark hyaline (winter growth) regions. The annular rings



in the sacculus. Lines drawn on the otoliths and scales show annular growth.

at this site are, for the most part, continuous and distinct. The annular markings on the scales are not as distinct or as sharp in contrast as on the otoliths. The scale annuli from the first three ages are well defined, but in ages 6 and 7 the outer annuli start to run together and the scale margin shows wear from resorption and deterioration. In contrast, the age-6 and -7 otoliths still reveal distinct annular rings.

PA, APE, and V values for all 10 treatments are presented by treatment comparisons in Table 1. The scale vs. otolith treatments were compared to determine how similar the two readers were in interpreting scale and otolith annuli. The PA values (82.6%, 80.4%) are relatively close to one another along with the values for APE and V. These values did reveal that R_1 had more agreement and less variability between aging scales and otoliths than did R_2. Table 1b shows a higher percentage agreement and less variability between R_1 and R_2 for otoliths than for scales.

Comparisons made between treatments of scales to true age and treatments of otoliths to true age are shown in Table 1c. The agreement of otolith ages to true ages was 10% greater and had half the variation of scale ages. Treatment comparison between male and female scale values were about the same (Table 1d), whereas the otolith values between sexes are quite different (Table 1e). The female otolith treatment had a higher PA value and lower APE and V values than did the male treatment.

Discussion

The scale vs. otolith treatment (Table 1a) revealed no real difference in the aging ability of each reader. There were also higher PA and lower V values for the treatment of otolith to true age (Table 1c). Therefore, the outcome for other treatments could be attributed to differences in the aging methods rather than the aging ability of the readers.

The results of the statistical tests (Table 1b) suggest that the method of estimating alewife ages from otoliths is superior to the method using scales. Ages derived from otoliths revealed a higher reproducibility and less variability than those obtained from scales. These differences between methods were inherent within the otoliths of female alewives, which provided the greatest accuracy and lowest variability (Table 1e) within all types of statistical comparisons.

Female alewives, at one time during their lives, possibly achieve a faster rate of growth than males. Cooper (1961), Havey (1961), and Libby (1982) showed that females are larger than males at age. This attribute of females would have the same effect on the growth of the otolith resulting in wider opaque zones with more distinct hyaline rings than male otoliths. Female scales would also have greater growth but possibly because of scale resorption and deterioration they were less easy to read than otoliths.

Other investigators have mentioned the ease of interpreting annuli of otoliths compared with scales, but have remarked that otoliths are less convenient to collect and store (Norden 1967; Kornegay 1978). The method presented in this paper was found to be more effective in obtaining both otoliths, unbroken, than the commonly used transverse cut made to the side of the head. The method of storage eliminated transferring and handling individual otoliths each time they were used. A disadvantage in using otoliths was that the fish had to be sacrificed. More care was required initially to obtain otoliths than scales, but the technique was quickly learned. The use of otoliths for aging alewives was more accurate and less subjective than aging with the use of scales.

Acknowledgments

I wish to thank Sherry Collins, Maine Department

TABLE 1.—Percent agreement (PA), average percent error (APE), and mean coefficient of variation (V) values for five treatment comparisons: a) scales and otoliths for R_1 against R_2; b) scales of R_1 and R_2 against otoliths of R_1 and R_2; c) scales of R_1 and R_2 and true age against otoliths R_1 and R_2 and true age; d) scales of R_1 and R_2 for males against scales of R_1 and R_2 for females; and e) otoliths of R_1 and R_2 for males against otoliths of R_1 and R_2 for females. S = scales; O = otoliths; 1 = R_1; 2 = R_2; A = true age.

	Treatment cmparisons									
	a		b		c		d		e	
	S_1O_1	S_2O_2	S_1S_2	O_1O_2	S_1S_2A	O_1O_2A	$S_1S_2\sigma$	$S_1S_2\varphi$	$O_1O_2\sigma$	$O_1O_2\varphi$
PA	82.6	80.4	85.0	89.0	78.8	87.7	84.0	85.8	86.5	92.2
APE	1.9	2.3	1.8	1.1	2.1	1.2	1.9	1.6	1.5	0.8
V	2.7	3.2	2.5	1.6	2.8	1.5	2.7	2.3	2.1	1.2

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Literature Cited

BEAMISH, R. J., AND D. A. FOURNIER.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982-983.

CHANG, W. Y. B.
1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208-1210.

COOPER, R. A.
1961. Early life history and spawning migration of the alewife, *Alosa pseudoharengus*. M.S. Thesis, Univ. Rhode Island, Kingston, 58 p.

HAVEY, K. A.
1961. Restoration of anadromous alewives at Long Pond, Maine. Trans. Am. Fish. Soc. 90:281-286.

KORNEGAY, J. W.
1978. Comparison of ageing methods for alewife and blueback herring. North Carolina Dep. Nat. Resour. Community Dev., Div. Mar. Fish., Spec. Sci. Rep. 30.

LIBBY, D. A.
1982. Decrease in length at predominant ages during a spawning migration of the alewife, *Alosa pseudoharengus*. Fish. Bull., U.S. 80:902-905.

MARCY, B. C., JR.
1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Trans. Am. Fish. Soc. 98:622-630.

NORDEN, C. R.
1967. Age, growth and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Trans. Am. Fish. Soc. 96:387-393.

PRICE, W. S.
1978. Otolith comparison of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill). Can. J. Zool. 56:1216-1218.

ROTHSCHILD, B. J.
1963. A critique of the scale method for determining the age of the alewife, *Alosa pseudoharengus* (Wilson). Trans. Am. Fish. Soc. 92:409-413.

WATSON, J. E.
1964. Determining the age of young herring from their otoliths. Trans. Am. Fish. Soc. 93:11-20.

WILLIAMS, T., AND B. C. BEDFORD.
1974. The use of otoliths for age determinations. *In* T. B. Bagenal (editor), The ageing of fish, p. 114-123. Unwin Brothers Limited, Surrey, Engl.

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PROBABLE CAUSES OF THE RAPID GROWTH AND HIGH FECUNDITY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER[1]

The introduction of walleye, *Stizostedion vitreum vitreum*, into the Pacific Northwest of the United States is not documented; however, they are now found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin[2]). The construction of dams has transformed the Columbia River from a free-flowing river into a series of low water-velocity impoundments with physical characteristics (Table 1) that closely match the model for ideal walleye habitat proposed by Kitchell et al. (1977a).

We studied basic life history factors of mid-Columbia River walleye for 2 yr to determine how well these exotic predators have adapted to their new environment. We found that our walleye grew at a rate approaching the highest previously reported, that they were highly fecund, and that they matured at an early age. We evaluated these high growth and reproductive rates against environmental and genetic variables. We believe these data will help to identify the ever increasing role of walleye in the aquatic ecosystem of the Columbia River and similar river-reservoir systems.

[1]Technical paper no. 6723, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

[2]Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, P.O. Box 3503, Portland, OR 97208. Mimeogr., 3 p.

FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980-81.

TABLE 1.—Summary of limnological data for the John Day pool of the Columbia River, from Hjort et al. (1981). All data collected in August 1979 except for surface temperatures, which were taken in 1981.

Characteristic	Range for John Day pool	Range for study area
Water velocity (m/s)	0.1-1.4	0.5-1.4
Secchi depth (m)	1.0-2.2	1.5-1.7
Dissolved O_2 (ppm) surface-bottom	16.0-8.0	14.0-10.0
Average surface temp. Apr.-July-Sept. (max.)	7.0°-24.5°-20.5°(24.8°)C	
Temperature profile surface-bottom	22.0°-20.8°C	21.0°-21.0°C
Pool width (km)	0.8-4.2	0.8-1.8
Mid-pool depth (m)	11-48	11-20
Pool length (km)	120	23

Methods

We collected walleye for this study in the first 23 km (tailrace) downstream of McNary Dam in the John Day pool of the Columbia River at lat. 45°55'N (Fig. 1). Walleye were collected from 2 April to 30 September 1980 and from 30 March to 30 September 1981. In 1980, we captured walleye with either a 38.1 × 1.8 m sinking gill net with 3.81, 5.08, 6.35, 7.52, and 10.16 cm variable stretch mesh, or a 76.2 × 3.7 m monofilament floating gill net with 15.25 cm stretch mesh. All gill net sets were of a maximum 2.5-h duration. In 1981 we used these gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front-mounted electrodes, utilizing pulsed DC current of 1-4 A to capture walleye. Sampling was conducted in the day and night.

We recorded the fork length (FL, mm), weight (g), sex and whether or not the fish were sexually mature (Eschmeyer 1950), and removed a scale sample from beneath the tip of the left pectoral fin of each walleye. Many authors report difficulty using scales to determine the age of older walleye (Carlander and Whitney 1961; Campbell and Babaluk 1979); therefore, we took a subsample of sagitta (n = 86), which we preserved in 50:50 glycerine and water.

We mounted scales between two glass microscope slides and viewed them using a microfiche projector at 43×. We identified annuli using the criteria described by Carlander and Whitney (1961). We found that the easiest way to detect annuli on sagittae was to burn the whole otolith in a flame, immerse it in oil or alcohol, and examine it under a dissecting microscope. Reburning was often necessary until very distinct, dark annuli appeared. Christensen (1964) proposed a similar technique; however, he broke the burned otolith and examined the cross section. There was 92% agreement between at least one otolith reading and one scale reading so we terminated the collection of otoliths. We examined scales and otoliths twice and a person experienced in reading walleye scales (W. R. Nelson, U.S. Fish and Wildlife Service, Vancouver, WA) examined a subsample of scales (n = 63).

Age determinations for walleye collected in 1980 were based on either two scale readings, three scale readings, two scale readings and two otolith readings, or three scale readings and two otolith readings. All age determinations of walleye collected in 1981 were based on two scale readings. There was 90% agreement between at least two of the five possible age determinations for walleye collected in 1980, and 75% agreement between the two age determinations for walleye collected in 1981. After the final age determination, we measured the scale radius and scale length to each annulus (43×) at about 45° off of a straight line from the focus through the anterior field. In this area of the scale it was much easier to detect the annuli because of crowding and anastomosis of circuli in the lateral fields.

We back-calculated length at each annulus (i.e., year of life) assuming a straight line body-scale relationship (r^2 = 0.69) and using the Fraser-Lee method as recommended by Carlander (1982):

$$L_i = a + \frac{(L_c - a)}{S_c} S_i$$

where L_c = fish fork length at capture
L_i = calculated fork length at age i
S_c = scale radius at capture
S_i = scale measurement at annulus i
a = intercept of body-scale regression = 55 mm.

We converted these back-calculated fork lengths to total lengths (TL) using a conversion factor of 1.06 FL, which is the unweighted mean of the TL/FL relationships reported by Colby et al. (1979). This conversion allowed us to more easily compare our data with data from other areas.

During the spring 1981 spawning season, we removed the ovaries from 27 mature, but unspawned walleye. We preserved the ovaries in Bouin's solution and subsequently estimated the number of eggs by means of the gravimetric method recommended by Wolfert (1969). We performed regressions of life

history characteristics by use of an interactive statistical computer program.

Results

We sampled over 250 walleye in each year, and they varied in length from 208 to 765 mm FL (220-810 mm TL) (Fig. 2). The weight (WT)/length (FL) relationship for 324 walleye was best described by the equation:

$$\text{Log}_e \text{WT} = -11.426 + 3.010 \text{ Log}_e \text{FL} \ (r^2 = 0.966).$$

The slopes and intercepts of similar weight-length regressions for walleye collected in 1980 versus 1981 and males versus females were not significantly different ($F = 4.61$; $\alpha = 0.01$; df = 2; 247).

We had no difficulty detecting annuli in the scale samples from older walleye because of their rapid growth and apparently short life span (Table 2). Although females are larger than males in each year of life, the difference is not statistically significant until after the second year.

The mean fecundity of 27 walleye, between 520 to 764 mm FL and 1,720 to 5,905 g weight, was 82,900 eggs/kg body weight (Table 3). We found fecundity (FEC) linearly related to fish weight (WT):

$$\text{FEC} = -28{,}100 + 93.8 \text{ WT}, \quad r^2 = 0.969$$

and curvilinearly related to fork length (FL):

$$\text{Log}_e \text{FEC} = -8.4 + 3.2 \text{ Log}_e \text{FL}, \quad r^2 = 0.905.$$

A majority of males and females were mature by age III (Fig. 3); however, the maturity at fork length data show a more gradual increase than do the maturity

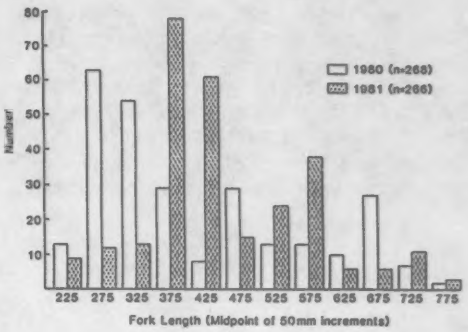

FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April-September 1980-81.

TABLE 2.—Average back-calculated fork length (FL), SE, and annual growth increment for walleye collected in the John Day pool of the Columbia River, April-September 1980-81.

	Age							
	I	II	III[1]	IV[1]	V[1]	VI[1]	VII[1]	VIII
Males								
FL (mm)	241	363	434	484	533	562	596	
SE	2	3	6	7	9	10	7	
N (cumulative)	134	86	35	25	21	18	8	
increment (mm)	241	122	71	50	49	29	34	
Females								
FL (mm)	243	371	456	527	590	643	684	701
SE	2	3	4	4	5	5	6	11
N (cumulative)	197	150	122	95	69	57	28	8
increment (mm)	243	128	95	61	62	54	41	17
Combined[2]								
FL (mm)	244	368	458	515	575	623	664	701
SE	2	2	3	4	4	5	8	11
N (cumulative)	446	277	189	142	104	85	40	8
increment (mm)	244	124	90	57	60	8	41	37

[1]Females versus males significantly different, $P < 0.01$, Student's *t*-test.
[2]Includes some fish whose sex was not determined.

TABLE 3.—Fecundity of walleye from the John Day pool of the Columbia River, 30 March to 18 April 1981, compared with fecundities from Norris Reservoir, TN (Smith 1941), Lake Gogebic, MI (Eschmeyer 1950), and western Lake Erie (Wolfert 1969).

		Eggs/kg body weight[1]	
Location	*N*	Range[1]	Mean[1]
John Day pool	27	69,000-101,000	82,900 ± 1,550 (1SE)
Norris Reservoir		28,400-32,700	29,700
Lake Gogebic	34	57,900-67,800	61,800
Western Lake Erie	78	56,300-123,200	82,500

[1]Values converted from eggs/pounds body weight and rounded to nearest 100 eggs, except John Day pool.

data by age and, inexplicably, males were not 100% mature at any length (Fig. 3).

Discussion

The transplanted walleye population of the John Day pool of the Columbia River grows at a rate approaching the highest previously reported (Fig. 4). Concomitant with rapid growth these walleye are very fecund (Table 3) and mature at an early age (Fig. 3). We suggest that these life history characteristics result from the combination of a favorable temperature regimen and a nonlimiting food supply.

High growth rates are generally found in walleye populations of more southerly latitudes where higher temperatures and longer growing seasons occur. Figure 4 contains data from Norris Reservoir, TN (Stroud 1949), Lake Gogebic, MI (Eschmeyer 1950), Lac la Ronge, Saskatchewan (Rawson 1957); as well as the composite high and low length-at-age values reported by Colby et al. (1979). Relative to the latitude of the John Day pool (lat. 45°55′N), Norris Reservoir is south (lat. 36°15′N), Lac la Ronge is north (lat. 55°07′N), and Lake Gogebic is at approximately the same latitude (lat. 46°47′N). The mean growing degree-days (GDD) above 5°C (GDD >5°C)

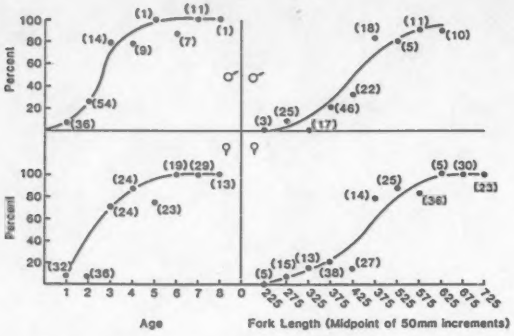

FIGURE 3.—Percent mature walleye by age and length and by sex for specimens collected in the John Day pool of the Columbia River, April-September 1980-81. Curves were drawn by eye. (Sample size in parentheses.)

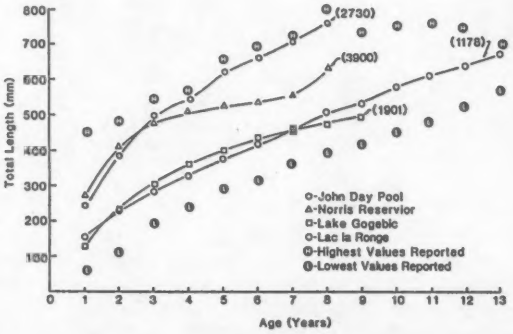

FIGURE 4.—Comparison of length-at-age for walleye from the John Day pool, Columbia River; Norris Reservoir, Tennessee (Stroud 1949); Lake Gogebic, Michigan (Eschmeyer 1950); Lac la Ronge, Saskatchewan (Rawson 1957) and the composite high and low values reported by Colby et al. (1979). Numbers in parentheses are the mean growing degree-days above 5°C, John Day value is from Anonymous (1969), all others are from Colby and Nepszy (1981).

(Colby and Nepszy 1981) for each area are included in Figure 4 as a measure of solar energy input to the system. Colby and Nepszy (1981) found that walleye growth was directly correlated to GDD >5°C and that the optimum range was from 2,500 to 4,000 GDD >5°C. While the GDD >5°C for the John Day pool is within this range, the walleye growth reported here is greater than would be predicted using this variable.

Water temperature may be the most important factor governing the growth of fishes (Brett 1979). Kitchell et al. (1977b) presented a bioenergetics model for walleye growth and indicated that thermal optima and maxima for weight specific consumption are 22°C and 27°C, respectively, and 27°C and 32°C, respectively, for weight specific respiration. Water temperatures in the John Day pool during the growing season remain at or near the thermal optimum for consumption and, perhaps more importantly, do not approach the thermal maxima for consumption or respiration (Table 1). Many northern lakes may not reach the thermal optima (Rawson 1957; Swenson 1977) and the southern lakes or lakes which stratify in the summer may exceed the thermal maxima (MacLean and Magnuson 1977) not only reducing consumption but increasing respiration. Dendy (1948) reported that in June 1944 the surface temperature of Norris Reservoir was about 30°C and that walleye appeared to prefer water temperature of about 24°C, even though these areas had oxygen concentrations <3.0 mg/L. Conversely, water temperature of Lac la Ronge did not exceed 20°C (Rawson 1957), well below the thermal optima.

Exceptions to the north-south trend in high walleye growth occur in systems of high exploitation (Forney 1965) and/or where there have been decreases in interspecific competition (Wolfert 1969; Forney 1977) which results in density dependent increases in growth rates. The quantity and quality of food are important factors in walleye growth (Kelso 1972; Kerr and Ryder 1977; Kitchell et al. 1977b) and fecundity (Colby and Nepszy 1981). Schupp (1978) looked at the growth of walleye from several areas within Leech Lake, MN, and found food of walleye from areas of highest average growth was almost totally young-of-the-year yellow perch, whereas small walleyes from slow growth areas had eaten mostly invertebrates and small minnows. We have found (Maule and Horton 1984) that about 99% by volume of Columbia River walleye stomach contents were fish (e.g., sculpins, suckers, cyprinids) and that 61% of walleye sampled contained food. Eschmeyer (1950) reported that 89% of the volume of stomach contents from Lake Gogebic walleye was fish, but he did not report percent empty stomachs. Dendy (1946) reported that Norris Reservoir walleye stomachs contained 99% fish by volume, but only 45% of the walleye examined contained food. Rawson (1957) studied Lac la Ronge walleye and reported that fish comprised 97% of the volume of stomach contents and that 39% of the walleye stomachs contained food.

Colby and Nepszy (1981) stated that age to maturity is indirectly correlated to growth, but that fecundity is probably a function of population density and food availability. They further suggested that the wide variability in walleye fecundities is a mechanism by which walleye can adjust production in response to environmental conditions. Table 3 includes fecundity data from Norris Reservoir (Smith 1941), Lake Gogebic (Eschmeyer 1950), and western Lake Erie (Wolfert 1969). Based on a comparison of growth, stomach content analysis, and fecundity, the mid-Columbia River walleye have a more favorable food supply than the other areas considered here.

Hackney and Holbrook (1978) suggested that there is a southern race of walleye that is characterized by rapid, large growth and short life span, and a northern race characterized by slow growth and long life span. They suggested that the pattern of rapid walleye growth seen after the impoundment of southern waters, followed by decreased growth rates some years later is due to a shift from the southern race to the northern race as the result of walleye stocking programs. The movements of young-of-the-year walleye downstream past Columbia River dams has been documented (Brege 1981). Assuming that this is a means by which walleye have colonized the Columbia River, it is biologically similar to impounding waters already containing walleye populations, in that new habitat is available for population growth. Although we cannot discount the possibility that the extreme life history characteristics reported here are the result of genetic stock differences, we suggest that they can more reasonably be explained by a favorable temperature regimen and an abundant, high quality food supply.

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Literature Cited

ANONYMOUS.
1969. Climatological handbook. Columbia Basin states. Temperature. Volume 1, part A. Meteorology Committee, Pacific Northwest River Basins Commission, Vancouver, WA, 268 p.

BREGE, D. A.
1981. Growth characteristics of young-of-the-year walleye, *Stizostedion vitreum vitreum*, in John Day Reservoir on the Columbia River, 1979. Fish. Bull., U.S. 79:567-569.

BRETT, J. R.
1979. Environmental factors and growth. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology. Volume VIII. Bioenergetics and growth, p. 599-676. Acad. Press, N.Y.

CAMPBELL, J. S., AND J. A. BABALUK.
1979. Age determination of walleye, *Stizostedion vitreum vitreum*, (Mitchill), based on the examination of eight different structures. Can. Fish. Mar. Serv., Tech. Rep. 849, 23 p.

CARLANDER, K. D.
1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. Trans. Am. Fish. Soc. 111:332-336.

CARLANDER, K. D., AND R. R. WHITNEY.
1961. Age and growth of walleyes in Clear Lake, Iowa, 1935-1957. Trans. Am. Fish. Soc. 90:130-138.

CHRISTENSEN, J. M.
1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Int. Counc. Explor. Sea 29:73-81.

COLBY, P. J., R. E. MCNICOL, AND R. A. RYDER.
1979. Synopsis of biological data on the walleye, *Stizostedion vitreum vitreum* (Mitchill 1818). FAO Fish. Synop. 119, 139 p.

COLBY, P. J., AND S. J. NEPSZY.
1981. Variation among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. Can. J. Fish. Aquatic Sci. 38:1814-1831.

DENDY, J. S.
1946. Food of several species of fish, Norris Reservoir, Tennessee. J. Tenn. Acad. Sci. 21(1):105-127.
1948. Predicting depth distribution of fish in three TVA storage-type reservoirs. Trans. Am. Fish. Soc. 75:65-71.

ESCHMEYER, P. H.
1950. The life history of the walleye, (*Stizostedion vitreum vitreum* (Mitchill)), in Michigan. Mich. Dep. Conserv., Bull. Inst. Fish. Sci. 3.

FORNEY, J. L.
1965. Factors affecting growth and maturity in a walleye population. N.Y. Fish Game J. 12:217-232.
1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34:1812-1820.

HACKNEY, P. A., AND J. A. HOLBROOK II.
1978. Sauger, walleye, and yellow perch in the southwestern United States. *In* R. L. Kendall (editor), Selected coolwater fishes of North America, p. 74-81. Am. Fish. Soc. Spec. Publ. 11.

HJORT, R. C., B. C. MUNDY, AND P. L. HULETT.
1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Final report. U.S. Army Corps Eng. Contract No. DACW57-79-C-0067. Portland, OR.

KELSO, J. R. M.
1972. Conversion, maintenance and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet and temperature. J. Fish Res. Board Can. 29:1181-1192.

KERR, S. R., AND R. A. RYDER.
1977. Niche theory and percid community structure. J. Fish. Res. Board Can. 34:1952-1958.

KITCHELL, J. F., M. G. JOHNSON, C. K. MINNS, K. H. LOFTUS, L. G. GREIG, AND C. H. OLVER.
1977a. Percid habitat: The river analogy. J. Fish. Res. Board Can. 34:1936-1940.

KITCHELL, J. F., D. J. STEWART, AND D. WEININGER.
1977b. Applications of bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922-1935.

MACLEAN, J., AND J. J. MAGNUSON.
1977. Species interactions in percid communitites. J. Fish. Res. Board Can. 34:1941-1951.

MAULE, A. G., AND H. F. HORTON.
1984. Feeding ecology of walleye, (*Stizostedion vitreum vitreum*) in the mid-Columbia River, with emphasis on the interactions between walleye and juvenile anadromous fishes. Fish. Bull., U.S. 82:411-418.

RAWSON, D. S.
1957. The life history and feeding ecology of the yellow walleye, *Stizostedion vitreum*, in Lac la Ronge, Saskatchewan. Trans. Am. Fish. Soc. 86:15-37.

SCHUPP, D. H.
1978. Walleye abundance, growth, movement, and yield in disparate environments within a Minnesota Lake. *In* R. L. Kendall (editor), Selected coolwater fishes of North America, p. 58-65. Am. Fish. Soc. Spec. Publ. 11.

SMITH, C. G.
1941. Egg production of walleyed pike and sauger. Norris Reservoir fish differ from same species in other localities. Prog. Fish-Cult. 54:32-34.

STROUD, R. H.
1949. Growth of Norris Reservoir walleye during the first twelve years of impoundment. J. Wildl. Manage. 13:157-177.

SWENSON, W. A.
1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34:1643-1654.

WOLFERT, D. R.
1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. J. Fish. Res. Board Can. 26: 1877-1888.

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BIOLOGICAL ASPECTS OF THE SPRING BREEDING MIGRATION OF SNOW CRABS, *CHIONOECETES OPILIO*, IN BONNE BAY, NEWFOUNDLAND (CANADA)

The occurrence of an annual (April-May) deep- to shallow-water breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, on the west coast of Newfoundland, has been documented by Hooper (in press). In addition to being the first record of this phenomenon in this species, his observations contradict some generally accepted conclusions regarding the species' reproductive biology. The most significant of these are that females undergo a terminal molt to maturity and do not mate in the hard shell condition (Ito 1967; Watson 1972; Takeshita and Matsuura 1980).

Little morphometric sampling data are included in Hooper's general description of the breeding migration. The purpose of this paper is to provide a more detailed description of various biological aspects of the phenomenon, such as size difference between paired males and females, and condition of the external egg masses, ovaries, and spermathecae during the breeding period.

Materials and Methods

Three hundred and three sexually paired snow crabs were collected during three field trips to Bonne Bay from 24 April to 29 May 1984 by scuba diving (10-30 m depth). Each pair was kept in a separate mesh bag. At the surface, each crab was measured to the nearest millimeter (maximum carapace width (CW)) and its shell condition (soft, new/hard, or old/hard) determined. The eggs of females were examined to determine their stage of development. Following this, males were tagged with Floy vinyl "T-bar" tags (Taylor 1982) and released, and females were either tagged and released, or retained for later examination of their ovaries and spermathecae in the laboratory.

Results

Size Distribution

Size distributions were unimodal for each sex but with no overlap in their carapace widths (Fig. 1). Males ranged from 89 to 140 mm ($\bar{x}$ = 116.4 mm) CW and females from 55 to 86 mm ($\bar{x}$ = 67.8 mm). Other than the fact that males were invariably larger than females, there was no discernible relationship between size of the male and size of the female with which it was paired (Fig. 2). Mean sizes of females paired with small, medium, and large size males were the same ($P < 0.005$, Bartlett's test of homogeneity of variance).

Male CW (mm) *Range*	*Female CW (mm)* *Range*	*Mean*	N
89-109 (small)	55-86	69.2	59
110-120 (medium)	59-86	69.6	136
121-120 (large)	59-84	70.9	108
		Total	303

The mean difference in carapace width between paired males and females increased from 21 mm at 89 mm male CW to 70 mm at 140 mm. Only 3 males in 303 pairs were smaller than 95 mm, the legal size limit.

Female Reproductive Condition

During the 24-27 April sampling period, 92% of the females carried full clutches of eyed eggs and the remainder had liberated all or most of the larvae (Table 1). By 7-11 May, 59% had empty brood pouches indicating that hatching was well advanced. However, during 22-25 May, 53% of the females were carrying full clutches of eyed eggs and only 39% had empty brood pouches. This increase in relative abundance of females with eyed eggs could have resulted from a return to deeper water of females that had liberated larvae or an influx of new animals from deeper water. Dead eggs were carried by 1.4% of females examined. All females dissected (77) had ripe (extrusion imminent) ovaries (Table 2); however, only two with partially extruded clutches

TABLE 1.—Summary of observations on external egg masses of female *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, April-May 1984.

Sampling period	Eyed (%)	Larvae liberating (%)	Larvae liberated (%)	*N*
24-27 April	92	0	8	128
7-11 May	9	32	59	81
22-25 May	53	8	39	87

TABLE 2.—Summary of internal observations on female *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, April-May 1984.

Sampling period	Ripe ovaries (%)	Spermatophores (%)			*N*
		Old only	Old and new	New only	
24-27 April	100	45.7	48.6	5.7	35
22-25 May	100	7.1	92.9	0	42

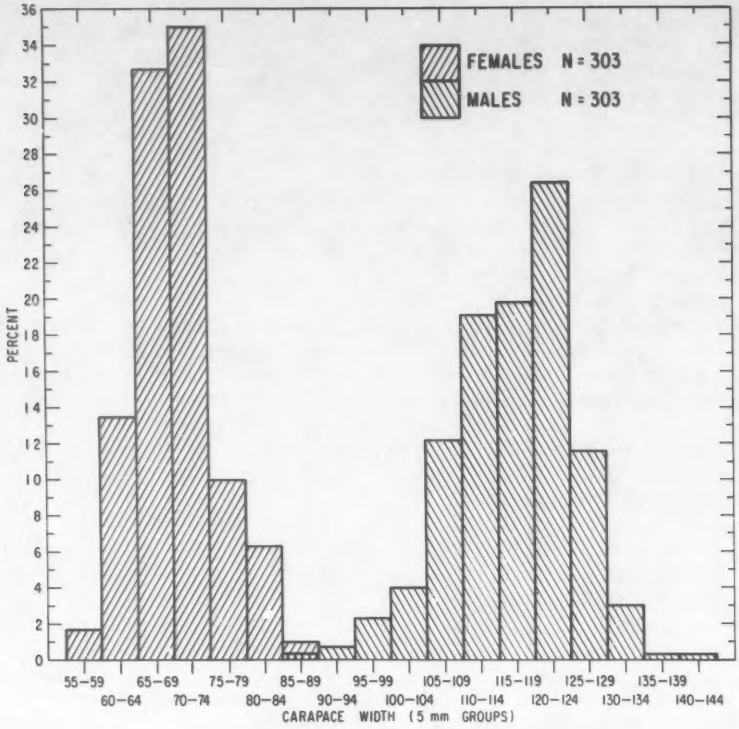

FIGURE 1.—Size-frequency distributions of male and female *Chionoecetes opilio* collected as pairs in Bonne Bay, Newfoundland, during April-May 1984.

of new eggs were found over the entire sampling period.

Females were observed with spermathecae containing both old and new spermatophores. In these, spermathecae were engorged with a very white glutinous material containing new spermatophores for three-fourths of their length, while the remaining one-fourth at the dorsal end of the organ was shrunken and contained a yellowish brown substance of a "waxy" consistency. Females which did not have new spermatophores had very small spermathecae which were entirely yellowish brown in color. This is very similar to that described for *Chionoecetes bairdi* by Paul (1982). While 97% of all females examined contained old spermatophores, those containing new spermatophores as well increased to 92.9% from 48.6% between 24 April and 25 May (Table 2). Two specimens contained new spermatophores only and all had old epizooite-encrusted shells. Thirty-six percent of the females with new spermatophores carried full clutches of eyed eggs.

Diving during 28-31 May revealed that all crabs had left the sampling area.

Discussion

Small numbers of grasping, male/female pairs of *C. opilio* and *C. bairdi* have been observed in shallow water elsewhere. Ennis (Unpubl. data) found five pairs and Hooper (Unpubl. data) found three pairs of *C. opilio* in Bonavista Bay and Placentia Bay, Newfoundland, respectively. Donaldson (1975) reported two pairs of *C. bairdi* in Alaska. However, nothing comparable with the magnitude of the breeding migration of *C. opilio*, observed in Bonne Bay, Newfoundland, has been reported for other areas. There is considerable scope for speculation on the ecological significance of this migration. Although about half the females examined just prior

to their departure from the shallow (<35 m) sampling depths in 1984 still had full clutches of eyed eggs, liberation of a large proportion of larvae in shallow water may enhance chances for larval survival overall. At the time of the migration, bottom temperatures in Bonne Bay at depths beyond 35 m are probably 0°C or lower [deep water temperatures are not available for Bonne Bay but Squires et al. (1971) reported temperatures <0°C at depths beyond 30 m in early June in North Arm, Bay of Islands, about 40 km to the south]. Release of larvae in shallow, warmer water (temperature was 3°C at 30 m during 7-11 May) would considerably reduce the degree of thermal shock associated with larvae swimming to the surface. The rate of embryonic development would likely be increased also, resulting in earlier larval release.

In the development of a management strategy for *C. opilio* stocks on the Atlantic coast of Canada, a key assumption has been that, despite high levels of exploitation, reproductive potential in a stock remains at prefishery levels. The basis for the assumption is that females are protected from exploitation by the 95 mm CW minimum legal size because they do not grow to that size and also that males mature at sizes much smaller than 95 mm CW. In a recent review, following more than 15 yr of heavy fishing in some areas, there was no evidence to indicate that the assumption was invalid (Elner and Robichaud 1983). However, the observations presented here suggest that a large size differential between the male and female of a pair is an important element of behavioral interactions during breeding activity. It is possible that males smaller than 89 mm CW (the smallest male observed paired with a female), even though physiologically mature, may be less likely to mate successfully in competition with large males.

Males and females appear to be segregated over most of the year (Hooper in press). Observations on the east coast of Newfoundland indicate that large males occur mainly on muddy bottom in deep water whereas females and small males occur on sand-gravel or rocky bottom somewhat shallower (Miller and O'Keefe 1981). In the breeding migration which occurs in Bonne Bay, Hooper (in press) suggested that males leave the deeper water area after selecting a mature female which is carried to the shallow water breeding area. Males retain possession of individual females for extended periods (Hooper in

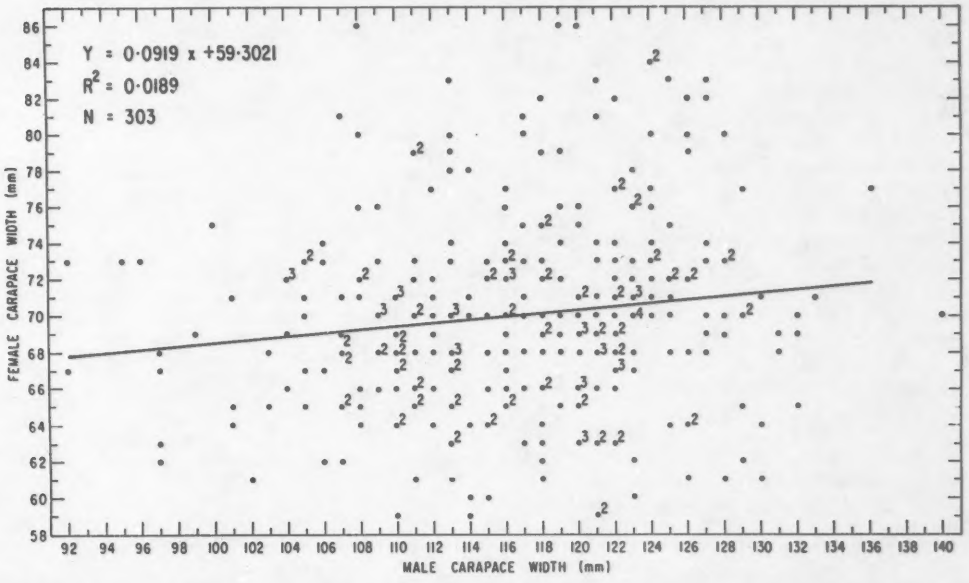

FIGURE 2.—Regression of female carapace width on male carapace width for pairs of *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, during April-May 1984. Numbers adjacent to points indicate more than one observation. Slope of the regression is not significant (P = 0.017).

press) (possibly up to 2 mo) during which time the female is held by and dependent on the male. In laboratory studies on *C. bairdi*, Paul and Adams (1984) demonstrated that multiparous females are receptive to mating for periods ranging from <1 to 7 d after all their eggs have hatched. In fact, they reported that only one ovigerous female mated successfully during their study.

In the Gulf of St. Lawrence, male snow crabs mature within the 50-65 mm CW size range (Powles 1968; Watson 1970); however, in the sampling reported here, only 3 males from the 303 pairs examined were smaller than the 95 mm CW minimum legal size, the smallest being 89 mm. Except for these, even solitary males of this size and smaller were absent from the area indicating that competition for females had occurred in deeper water. This snow crab population appears to be small and is isolated from populations elsewhere in the Gulf of St Lawrence by the 35 m deep sill at the mouth of Bonne Bay. This area has not been fished commercially and at present the population is considered to be in the virgin state. Hooper's (in press) observations indicated there is keen competition between single males and males already paired with a female for possession of the female. Under prefishery conditions this competition can be expected to eliminate small males from participating in breeding activity. Adams (1982) demonstrated that multiparous female *C. bairdi* resisted mating attempts by small males, and when males of significantly different sizes competed for the same female, the larger male was invariably successful. Small numbers of the largest of the sublegal (<95 mm CW) male *C. opilio* appear to be capable of competing and mating successfully. However, it is presently unknown whether males smaller than those observed are capable of successful mating with multiparous females in the absence of competition from large males and, if they are not, whether there are sufficient numbers of large sublegal males to maintain full reproductive potential in a heavily fished population.

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Literature Cited

ADAMS, A. E.
1982. The mating behavior of *Chionoecetes bairdi*. *In* B. Melteff (editor), Proceedings of the International Symposium on the genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, p. 273-281. Univ. Alaska, Fairbanks, Sea Grant Rep. 82-10.

DONALDSON, W. E.
1975. Kodiak Tanner Crab Research. Technical Report for period July 1, 1974 to June 30, 1975. NOAA, NMFS, 69 p.

ELNER, R. W., AND D. A. ROBICHAUD.
1983. Observations on the efficacy of the minimum legal size for Atlantic snow crab, *Chionoecetes opilio*. CAFSAC Res. Doc. 83/63, 26 p.

HOOPER, R. G.
In press. A spring breeding migration of the snow crab (*Chionoecetes opilio*) into shallow water in Newfoundland. Crustaceana.

ITO, K.
1967. Ecological studies on the edible crab, *Chionoecetes opilio* O. Fabricius in the Japan Sea. I. When do female crabs first spawn and how do they advance into the following reproductive stage? Bull. Jpn. Sea Reg. Fish Res. Lab. 17:67-84. [Engl. transl. from Jpn. by Fish Res. Board Can. Trans. Ser. No. 1103.]

MILLER, R. J., AND P. G. O'KEEFE.
1981. Seasonal and depth distribution, size, and molt cycle of the spider crabs, *Chionoecetes opilio*, *Hyas araneus* and *Hyas coarctatus* in a Newfoundland bay. Can. Tech. Rep. Fish. Aquat. Sci. 1003, 18 p.

PAUL, A. J.
1982. Mating frequency and sperm storage as factors affecting egg production in multiparous *Chionoecetes bairdi*. *In* B. Melteff (editor), Proceedings of the International Symposium on the genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, p. 273-281. Univ. Alaska, Fairbanks, Sea Grant Rep. 82-10.

PAUL, A. J., AND A. E. ADAMS.
1984. Breeding and fertile period for female *Chionoecetes bairdi* (Decapoda, Majidae). J. Crustacean Biol. 4:589-594.

POWLES, H. W.
1968. Distribution and biology of the spider crab *Chionoecetes opilio* in the Magdalen Shallows, Gulf of St. Lawrence. Fish. Res. Board Can. MS Rep. 997, 106 p.

SQUIRES, H. J., G. E. TUCKER, AND G. P. ENNIS.
1971. Lobsters (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963-65. Manuscr. Rep. Ser. (Biol.) No. 1151, 58 p.

TAYLOR, D. M.
1982. A recent development in tagging studies on snow crab, *Chionoecetes opilio* in Newfoundland - Retention of tags through ecdysis. *In* B. Melteff (editor), Proceedings of the International Symposium on the genus *Chionoecetes*. Lowell Wakefield Fisheries Symposia Series, p. 405-417. Univ. Alaska, Fairbanks, Sea Grant Rep. 82-10.

TAKESHITA, K., AND S. MATSUURA.
1980. Mating and egg-laying in Tanner crabs. Bull. Far Seas Fish. Res. Lab.

WATSON, J.
1970. Maturity, mating and egg-laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27:1607-1616.
1972. Mating behavior in the spider crab, *Chionoecetes opilio*, J. Fish. Res. Board Can. 29:447-449.

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FEEDING, DIET, AND REPEAT SPAWNING OF BLUEBACK HERRING, *ALOSA AESTIVALIS*, FROM THE CHOWAN RIVER, NORTH CAROLINA

Current knowledge of the frequency of feeding among spawning blueback herring, *Alosa aestivalis* Mitchill, is limited. Other aspects of the blueback herring's life history have been more extensively studied: feeding of juveniles (Davis and Cheek 1966; Nichols 1966; Burbidge 1974; Domermuth and Reed 1980; Crecco and Blake 1983), distribution at sea (Hildebrand 1963; Holland and Yelverton 1973[1]; Neves 1981), and spawning range (Bigelow and Schroeder 1953; Hildebrand 1963; Scott and Crossman 1973). However, determination of the occurrence of feeding by adults in freshwater has received little attention despite the fact that spawning bluebacks are common in rivers from southern New England (Bigelow and Schroeder 1953) to the St. Johns River, FL (Hildebrand 1963). Throughout this extensive range only Frankensteen (1976) has studied feeding among adult bluebacks in freshwater. Furthermore, no attempt has been made to correlate feeding with length, weight, and sex of individual fish, distance upstream, or the number of seasons a blueback has spawned.

The objective of this study is to enhance our knowledge of the freshwater feeding of blueback herring. In this paper I describe the occurrence of feeding, diet, and percentage of repeat spawning among adults collected in the Chowan River, NC. I also examined, by multiple regression analysis, the relation between feeding activity in freshwater and length, weight, sex, the number of repeat spawnings, and the distance travelled upstream.

Materials and Methods

Collection of Data

Bluebacks were collected at two sites in the lower Chowan River system during April 1980 and 1981. Williams' Fishery, where five collections were made in 1980, is located on the lower Meherrin River near its junction with the Chowan River, 90 km upstream from the Chowan River's mouth. Rocky Hock Creek, where bluebacks were sampled twice in 1980 and once in 1981, is roughly 20 km from the mouth of the Chowan River. Bluebacks at Williams' Fishery were still migrating upstream while those at Rocky Hock Creek, a known spawning ground,[2] were preparing to spawn.

Bluebacks were caught in chicken-wire dip nets and fixed gill nets with 58 mm stretched mesh at Rocky Hock Creek. A drift gill net of similar mesh size and a haul seine were used at Williams' Fishery. None of the fish collected had spawned yet.

Bluebacks were measured, weighed, and sexed, and scales were removed for aging. The foregut and midgut regions of the stomach anterior to the pyloric caeca were removed and placed in 15% Formalin[3] within 10-15 min of capture.

Stomach contents were examined in the laboratory under a dissecting scope. First, fullness of the foregut and midgut, which are separate sections, was estimated visually following Hynes (1950) and Yoshiyama (1980). Five levels of fullness were used: half full (1/2), full (1), and distended with food (2) (as in Yoshiyama 1980), plus one quarter full (1/4), and empty or with traces of food (0). Contents of each section were then placed in a petri dish, identified, and counted. Also, the presence or absence of prey items was noted.

Scales were viewed at 50× through an EPO LP-2 Profile Projector and marks were interpreted following Marcy (1969).

[1]Holland, B. F., Jr., and G. F. Yelverton. 1973. Offshore anadromous fish exploratory fishing program. Completion report, Project AFC-5, 123 p. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sports Fisheries, Raleigh, NC 27611.

[2]S. Winslow, North Carolina Division of Marine Fisheries, Elizabeth City, NC 27909, pers. commun. February 1980. S. Winslow had determined the previous year (1979) that blueback herring collected at this site on Rocky Hock Creek were spawning. Also, a dam upstream prevented blueback herring from moving any further than 150 m above my collection site.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Statistical Analysis

To obtain a single index of stomach fullness, values for the foreguts and midguts were combined by using a weighted average. In calculating mean volumes each gut section was assumed to be approximately cylindrical. The foregut to midgut volume ratio, determined from five randomly chosen stomachs, was 3.16:1. The following equation was used to calculate the overall gut fullness:

$$\frac{F \times 3.16 + M}{4.16}$$

with F and M representing the foregut and midgut values, respectively.

A multiple regression (General Linear Model-Statistical Analysis Systems) was initially employed to determine which of the variables collected for each fish (i.e., distance upstream, length, weight, sex, and number of repeat spawnings) was most strongly correlated with stomach fullness, the dependent variable. Significant variables identified through multiple regression analysis were further analyzed with chi-square and F-tests.

Results

Presence of Food

Nearly all (91 of 103 or 88%) fish sampled in April 1980 contained food (Table 1) as did all 15 fish collected in April 1981. High percentages of the fish collected on each date in 1980 had food in their stomachs (Table 1). About 53% (48 of 91) of the bluebacks in 1980 (Table 1) and 73% (11 of 15) of the bluebacks in 1981 had either foregut and/or midgut fullnesses of 1/4 or greater. Approximately half of the fish from each date in 1980, with the exception of 13 April, had either foregut and/or midgut fullnesses of 1/4 or greater (Table 1).

Diet

The diet of the bluebacks collected in 1980 at both sites was composed of zooplankters, benthos, and terrestrial insects (Table 2). Chydorid cladocerans were the only zooplankters consumed in large numbers at either location (Figs. 1, 2). Insects, which accounted for 8.1% of the organisms consumed, occurred in about half of the fish. Ephemeroptera (*Baetis*), Coleoptera (Dytiscidae), and Heleidae larvae, as well as chironomid larvae and pupae, were the most conspicuous of the identifiable benthic insects. Most insects, benthic and terrestial, were unidentifiable. Chironomids occurred more frequently than other insect groups, but they accounted for only 2.7% of the total prey items. Several terrestrial insects were found in stomachs of bluebacks, particularly at Williams' Fishery. Insects, both benthic and terrestrial, increased in importance with time at Williams' Fishery, reaching about 22% during later collections (Fig. 1). Insects represented a smaller proportion of the diet at Rocky Hock Creek (Fig. 2). Fish eggs (probably from alewives or bluebacks), which occurred in the stomachs of several bluebacks in 1980 (Figs. 1, 2), were the most abundant food item in that year although their importance decreased with time. Varying amounts of sand and detritus occurred in many stomachs.

In 1981 the diet of bluebacks from Rocky Hock Creek was much less diverse (Table 3). Cladocerans, the predominant prey items, comprised 84.1% of the diet. Almost half of the prey items were daphnid

TABLE 1.—Incidence of feeding and stomach fullness in male and female blueback herring collected at Williams' Fishery (WF) and Rocky Hock Creek (RH) during April 1980.

Station and date of collection	No. fish collected per station	No. males (M) and females (F)		No. fish (n) with animal matter in stomach		No. of fish with ≥1/4 fullness for the foregut, midgut or both							
						Males			Females			Males + Females	
	N	M	F	n	% F	Fore	Mid	Both	Fore	Mid	Both	Total	% N
WF-4-5-80	16	8	8	12	75.0	0	1	0	1	2	3	7	43.6
RH-4-6-80	9	3	6	9	100.0	0	0	0	2	1	2	5	55.6
WF-4-7-80	17	8	9	15	88.2	1	3	0	0	2	3	9	52.9
WF-4-11-80	17	10	7	15	88.2	2	2	0	1	2	1	8	47.1
RH-4-12-80	7	6	1	7	100.0	1	1	0	0	0	1	3	42.9
WF-4-13-80	23	9	14	20	87.0	2	1	0	0	4	1	8	34.8
WF-4-19-80	14	10	4	13	92.9	0	5	0	0	2	1	8	57.1
Total	103	54	49	91	88.4	6	13	0	4	13	12	48	

cladocerans (Table 3). Few copepods were consumed, although they occurred in about half the fish. Ostracods were important numerically and in occurrence, as were daphnid ephippia. Benthic prey, terrestrial insects, fish eggs, detritus, and sand were rare.

TABLE 2.—Diets of 103 blueback herring collected at Williams' Fishery and Rocky Hock Creek during April 1980.

Prey taxon	Frequency of occurrence: No. of fish observed in	%	Proportions of prey items in diet: No. of prey	%
Copepoda				
Calanoida	1	1.0	1	(1)
Harpacticoida	5	4.9	12	0.4
Cyclopoida	35	33.9	80	2.8
Unidentifiable	7	6.8	21	0.7
Cladocera				
Chydoridae	61	59.2	839	29.6
Other families	14	13.6	26	0.9
Ostracoda	15	14.6	58	2.0
Insecta				
Miscellaneous	54	52.4	133	4.7
Diptera				
Chironomidae larvae	25	24.3	67	2.4
Chironomidae pupae	5	4.9	7	0.3
Other families	12	11.7	20	0.7
Oligochaeta	1	1.0	1	(1)
Mollusca				
Sphaeriidae	7	6.8	21	0.7
Fish eggs	43	41.8	1,273	44.9
Bryozoan statoblasts	20	19.4	178	6.3
Colonial hydrozoan pieces	16	15.5	96	3.4
Hydracarina	5	4.9	5	0.2
Total			2,838	100.0

1<0.1%.

TABLE 3.—Diets of 15 blueback herring collected at Rocky Hock Creek on 18 April 1981.

Prey taxon	Frequency of occurrence: No. of fish observed in	%	Proportions of prey items in diet: No. of prey	%
Copepoda				
Calanoida	5	33.3	8	0.1
Harpacticoida	7	46.6	7	0.1
Cyclopoida	7	46.6	23	0.4
Cladocera				
Daphnidae	15	100.0	3,191	48.7
Daphnidae ephippia	12	80.0	1,825	27.9
Chydoridae	13	86.6	493	7.5
Bosminidae	2	13.3	5	(1)
Ostracoda	13	86.6	929	14.2
Insecta				
Miscellaneous	5	33.3	6	0.1
Diptera				
Chironomidae larvae	5	33.3	8	0.1
Fish eggs	1	6.6	7	0.1
Bryozoan statoblasts	11	73.3	42	0.6
Hydracarina	3	20.0	3	(1)
Fish larvae	1	6.6	1	(1)
Total			6,548	99.8

1<0.1%.

Number of Repeat Spawnings

About 85% (87 of 103) of the fish in 1980 and 71% (10 of 14) in 1981 had spawned before (Table 4). Although some bluebacks in 1980 had spawned as many as six times, most (72%) had spawned only once or twice before (Table 4). Almost equal numbers of males (44) and females (43) were repeat spawners in 1980.

TABLE 4.—Number of previous years that 103 blueback herring collected at Williams' Fishery and Rocky Hock Creek during April 1980 had spawned.

	No. of years spawned					
	1 (first time)	2	3	4	5	6
Male	10	25	14	3	1	1
Female	6	22	13	6	2	0
Total	16	47	27	9	3	1

Relation Between Feeding Activity and Length, Weight, Sex, Number of Repeat Spawnings, and Distance Upstream

Sex was the only independent variable that contributed significantly to variance in feeding rate (Table 5). Female bluebacks fed more actively than males. The full model explained only 21% of the variance in gut fullness but this was significant ($F = 2.87, P > F = 0.005$, 102 df). The near significant contributions of length and weight to the reduction of variance in the model is believed to have resulted primarily from sex related differences in mean size ($\bar{x}$ length females = 305.1 mm, $\bar{x}$ length males = 289.4 mm; $\bar{x}$ weight females = 258.0 g, $\bar{x}$ weight males = 212.5 g). Further analysis of the feeding activity of male and female bluebacks with a chi-

TABLE 5.—Summary of the contribution of each of the independent variables to the multiple regression model for data from 103 blueback herring collected in 1980. Type IV *F* values and probability levels are shown. $P < 0.05$ significance level used.

Independent variable	*F* value	Probability
Site	2.64	0.1078
Sex	7.14	0.0089
No. of repeat spawnings	1.65	0.1818
Length	3.85	0.0527
Weight	3.81	0.0540

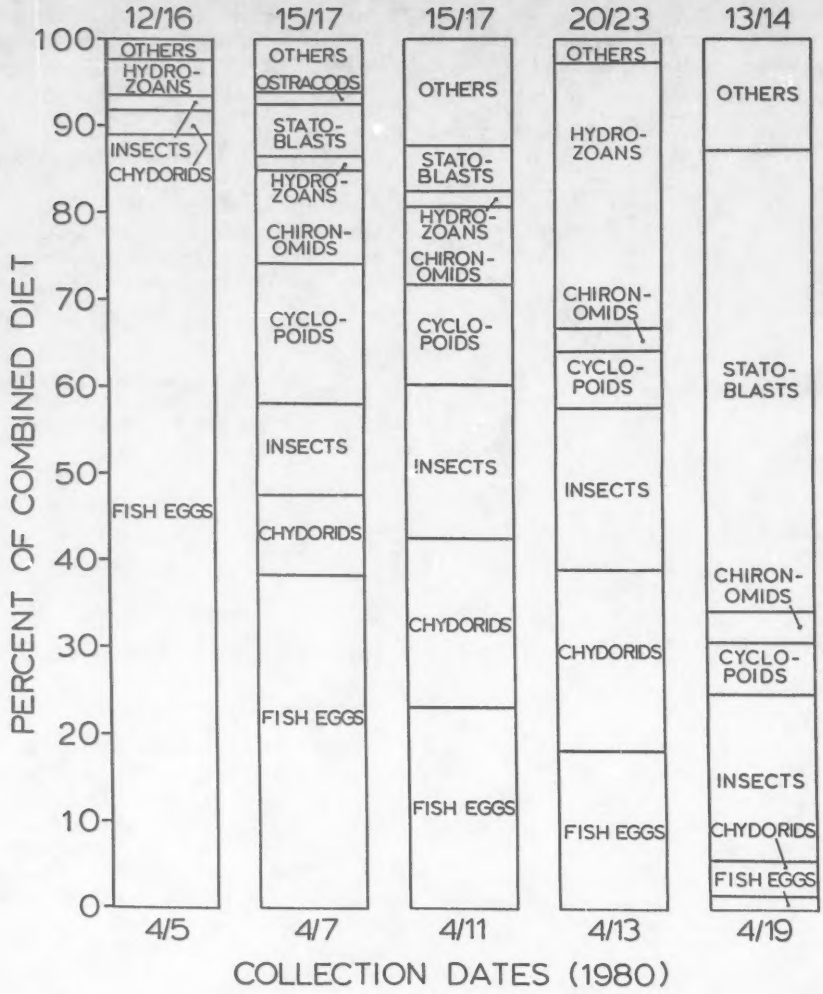

FIGURE 1.—Changes in the composition of the combined diet (both males and females) over the five collection dates at Williams' Fishery in April 1980. Numbers above each bar graph indicate number of stomachs with food/total number of stomachs examined.

square 2 × 2 contingency table also found significantly greater levels of feeding activity among females (χ^2 value = 5.86, $P < 0.025$). The difference in 1980, however, may depend on site. More females had stomach fullnesses ⩾1/4 than males at Rocky Hock (χ^2 value 6.349, $P < 0.025$), but the difference was not significant at Williams' Fishery.

For the three most abundant food items females consumed significantly greater numbers of chydorid cladocerans ($F = 6.02$, $P > F = 0.0001$), insects ($F = 7.64$, $P > F = 0.0001$), and fish eggs ($F = 90.15$, $P > F = 0.0001$) than males in 1980.

Discussion

Blueback herring spawning in the Chowan River do not stop feeding during their freshwater migrations. Williams' Fishery and Rocky Hock Creek are

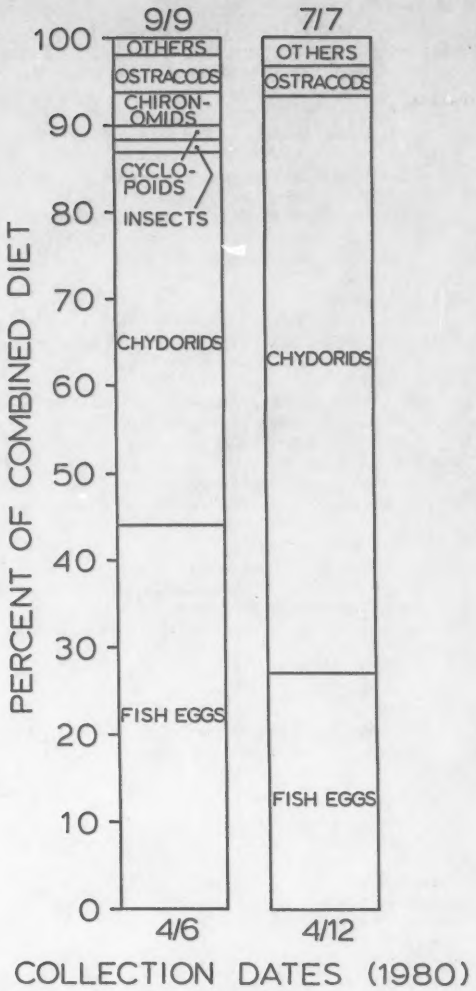

FIGURE 2.—Changes in the composition of the combined diet (both males and females) over the two collection dates at Rocky Hock Creek in April 1980. Numbers above each bar graph indicate number of stomachs with food/total number of stomachs examined.

too far from the estuary for bluebacks to travel to saltwater for daily feeding. It is important to note, also, that the interface between freshwater and saltwater often extends far out into Albemarle Sound due to the spring discharge of both the Chowan and Roanoke Rivers. This was the case in the spring of 1980.[4] Moreover, the prey were exclusively of freshwater origin. There is, therefore, little doubt that these bluebacks were feeding in freshwater.

The wide diversity of food items consumed was unexpected since bluebacks have previously been reported to be primarily planktivorous (Bigelow and Schroeder 1953; Hildebrand 1963). The limited 1981 data suggest that prey other than zooplankters are consumed infrequently if sufficient zooplankters (or large zooplankters such as *Daphnia*) are present. However bluebacks are also capable, as the 1980 data demonstrate, of foraging opportunistically on other riverine fauna and terrestrial insects, which could also explain Frankensteen's (1976) unusual finding that chironomids were the dominant prey of blueback herring in the Tar River. Consumption of benthic prey probably accounts for the presence of detritus and sand in the guts.

My data show a difference between male and female feeding activity. There are two possible explanations for this difference. First, females may require more energy than males during the spawning migration thus they consume more prey. Neither this study nor other studies of bluebacks have produced data to either support or refute this idea. However, moderate to severe weight loss is common among other spawning anadromous fishes (e.g., Atlantic salmon, American shad) with females suffering greater weight loss than males (Belding 1934; Chittenden 1976; Glebe and Leggett 1981). Glebe and Leggett (1981) found that development of ovaries in female shad required more energy and time than the male shads' testes. Consequently, female shad entering freshwater, particularly southern rivers, often do not have fully developed ovaries. Thus, not only must females expend energy for swimming but for gonad development as well. The same difference in gonad development may exist between male and female bluebacks and could explain the different levels of feeding activity observed in this study.

The second explanation for the difference in feeding activity is that all bluebacks, regardless of sex, stop feeding while spawning. However, males might remain on the spawning grounds longer than females. Thus, if females leave the area immediately after they spawn and are replaced by newly arrived females with relatively full guts, this could cause the gut samples to be biased. This explanation appears to be ruled out by the 1981 data, however, since half the fish with stomachs ≥1/4 full collected at Rocky Hock were males.

While previous researchers have found food in bluebacks' stomachs (Williams et al. 1975 as cited

[4]R. Holmes, Department of Natural Resources and Community Development, Division of Environmental Management, Raleigh, NC 27611, pers. commun. March 1984.

in Rulifson et al. 1982; Frankensteen 1976), my finding of a regular occurrence of significant volumes of food in blueback stomachs is unprecedented. Further research is needed to determine the extent to which feeding in freshwater is common among spawning bluebacks in other river systems, and possibly other anadromous species, and to determine if a relationship exists between freshwater feeding and spawning energetics.

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Literature Cited

BELDING, D. L.
1934. The cause of the high mortality in the Atlantic salmon after spawning. Trans. Am. Fish. Soc. 64:219-224.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

BURBIDGE, R. G.
1974. Distribution, growth, selective feeding, and energy transformations of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. Trans. Am. Fish. Soc. 103:297-311.

CHITTENDEN, M. E., JR.
1976. Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water. Fish. Bull., U.S. 74:151-157.

CRECCO, V. A., AND M. M. BLAKE.
1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Trans. Am. Fish. Soc. 112:498-507.

DAVIS, J. R., AND R. P. CHEEK.
1966. Distribution, food habits, and growth of young clupeids, Cape Fear River system, North Carolina. Proc. 20th Annu. Conf., SE Assoc. Game Fish. Comm., p. 250-259.

DOMERMUTH, R. B., AND R. J. REED.
1980. Food of juvenile American shad, *Alosa sapidissima*, juvenile blueback herring, *Alosa aestivalis*, and pumpkinseed, *Lepomis gibbosus*, in the Connecticut River below Holyoke Dam, Massachusetts. Estuaries 3:65-68.

FRANKENSTEEN, E. D.
1976. Genus *Alosa* in a channelized and an unchannelized creek of the Tar River basin, North Carolina. M.A. Thesis, East Carolina University, Greenville, NC, 123 p.

GLEBE, B. D., AND W. C. LEGGETT.
1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Can. J. Fish. Aquat. Sci. 38:806-820.

HILDEBRAND, S. F.
1963. Family Clupeidae. *In* H. B. Bigelow (editor), Fishes of the Western North Atlantic, Part 3, p. 257-454. Sears Found. Mar. Res., Yale University, New Haven, CT.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in the studies of the food of fishes. J. Anim. Ecol. 19:36-58.

MARCY, B. C., JR.
1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Trans. Am. Fish. Soc. 98:622-630.

NEVES, R. J.
1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *Alosa aestivalis*, along the Atlantic coast. Fish. Bull., U.S. 79:473-485.

NICHOLS, P. R.
1966. Anadromous Fishes Program. *In* Annual Report of the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., for the fiscal year ending June 30, 1966, p. 4-8. U.S. Fish Wildl. Serv. Circ. 264.

RULIFSON, R. A., M. T. HUISH, AND R. W. THOESEN.
1982. Anadromous fish in the southeastern United States and recommendations for development of a management plan. U.S. Fish Wildl. Serv., Fish. Res., Reg. 4, Atlanta, GA, 525 p.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184, 966 p.

YOSHIYAMA, R. M.
1980. Food habits of three species of rocky intertidal sculpins (Cottidae) in central California. Copeia 1980:515-525.

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19. Synopsis of biological data on the spottail pinfish, *Diplodus holbrooki* (Pisces: Sparidae). By George H. Darcy. January 1985, iv + 11 p., 8 figs.
20. Ichthyoplankton of the continental shelf near Kodiak Island, Alaska. By Arthur W. Kendall, Jr., and Jean R. Dunn. January 1985, iii + 89 p., 5 figs., 7 tables.
21. Annotated bibliography on hypoxia and its effects on marine life, with emphasis on the Gulf of Mexico. By Maurice L. Renaud. February 1985, iii + 9 p.
22. Congrid eels of the eastern Pacific and key to their leptocephali. By Solomon N. Raju. February 1985, iii + 19 p., 12 figs., 2 tables.
23. Synopsis of biological data on the pinfish, *Lagodon rhomboides* (Pisces: Sparidae). By George H. Darcy. February 1985, iv + 32 p., 22 figs., 24 tables.
24. Temperature conditions on the cold pool 1977-81: A comparison between Southern New England and New York transects. By Steven K. Cook. February 1985, iii + 22 p., 5 figs., 5 tables, 14 app. figs.
25. Parasitology and pathology of marine organisms of the world ocean. By William J. Hargis, Jr. (Editor). March 1985, iv + 135 p. [38 papers.]
26. Synopsis of biological data on the sand perch, *Diplectrum formosum* (Pisces: Serranidae). By George H. Darcy. March 1985, iv + 21 p., 20 figs., 7 tables.
27. Proceedings of the Eleventh U.S.-Japan Meeting on Aquaculture, Salmon Enhancement, Tokyo, Japan, October 19-20, 1982. By Carl J. Sindermann (Editor). March 1985, iii + 102 p. [15 papers.]
28. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. By William F. Perrin, Michael D. Scott, G. Jay Walker, and Virginia L. Cass. March 1985, iv + 28 p., 26 figs., 4 tables.
29. Prevalence, intensity, longevity, and persistence of *Anisakis* sp. larvae and *Lacistorhynchus tenuis* metacestodes in San Francisco striped bass. By Mike Moser, Judy A. Sakanari, Carol A. Reilly, and Jeannette Whipple. April 1985, iii + 4 p., 6 figs.
30. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. By Sandra E. Shumway, Herbert C. Perkins, Daniel F. Schick, and Alden P. Stickney. May 1985, iv + 57 p., 46 figs., 36 tables.

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ERRATA

Fishery Bulletin, Vol. 82, No. 2

Epperly, Sheryan P., and Walter R. Nelson, "Arithmetic versus exponential calculation of mean biomass," p. 446-448.

Page 446, left column, equation should read: $\bar{B}_t = \frac{B_t + B_{t+1}}{2}$

Page 446, right column, equation should read: $\bar{B}_t = \frac{\bar{B}_t\,(e^{G_t - Z_t} - 1)}{G_t - Z_t}$

447, left column, line 1, correct to read:

recruit. In one, $\bar{B}_t$ was computed arithmetically,

Page 447, right column, line 3, correct to read:

F-multiples and ages of entry, when $\bar{B}_t$ was cal-

Page 447, Figure 1, second line, correct to read:

when dt = 1.0 and B_t = 1.0, DELTA = $B_t(\bar{B}_{t,\,\mathrm{exp}} - \bar{B}_{t,\,\mathrm{arith}}) = B_t * \{0.0061 + 0.0037\,(G_t - Z_t) -$

Page 448, paragraph 1, line 8, correct to read:

ing a need to minimize the $G_t - Z_t$ difference if $\bar{B}_t$

Page 448, paragraph 1, last line, correct to read:

ommend that $\bar{B}_t$ be calculated exponentially.

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